THE BIOLOGY OF THE ECHINOID *EVECHINUS CHLOROTICUS* (VAL.)

IN DIFFERENT HABITATS

A thesis presented for the degree of

Doctor of Philosophy in Zoology

in the

University of Canterbury

Christchurch, New Zealand,

by

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1969

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1. INTRODUCTION

1.1 Previous work, aspects studied and aims

The general biology and ecology of the most common New Zealand shallow water echinoid Evechinus chloroticus (Val.) has been little studied. Papers to date discuss early distributional and taxonomic records (see Mortensen, 1943), suggestions as to the history of the genus (Fell, 1953), larval rearing experiments (Maxwell, 1957), detailed anatomy with biological notes (McRae, 1959), later distributional records (references, Section 1.3) and brief observations on seaweed grazing (Dromgoole, 1964).

The present study, which aimed to contribute to an understanding of the general biology and population ecology of Evechinus, has been facilitated by the use of SCUBA diving which brought the essentially subtidal populations within the reach of the author.

After initial surveys two major study areas which showed few, but marked, environmental differences, as well as marked differences in the size compositions of Evechinus populations, were selected for comparison. These areas were mainly subtidal localities around the Kaikoura Peninsula (42°25'S, 173°42'E) on the east coast, South Island, and subtidal and intertidal areas at Little Kaiteriteri, Kaiteriteri (42°02'S, 173°01'E) in Tasman Bay on the southern shores of Cook Strait, South Island (Fig. 1).

Kaikoura and Kaiteriteri differ in several respects:
(a) Hydrography. Kaikoura is situated near very deep water and is under fairly direct influence from oceanic currents. It is centred on a subtropical convergence of the Canterbury Current (subantarctic or cold temperate) and the East Cape Current (subtropical or warm temperate) (Knox, 1960). Although the hydrography of Kaiteriteri is little known, most of Tasman Bay is shallow (< 60m; A. N. Baker, pers. comm.), with localised current systems so that the area is only indirectly influenced by the D'Urville Current derived from the Westland Current of modified subtropical water. It follows that sea temperatures are warmer

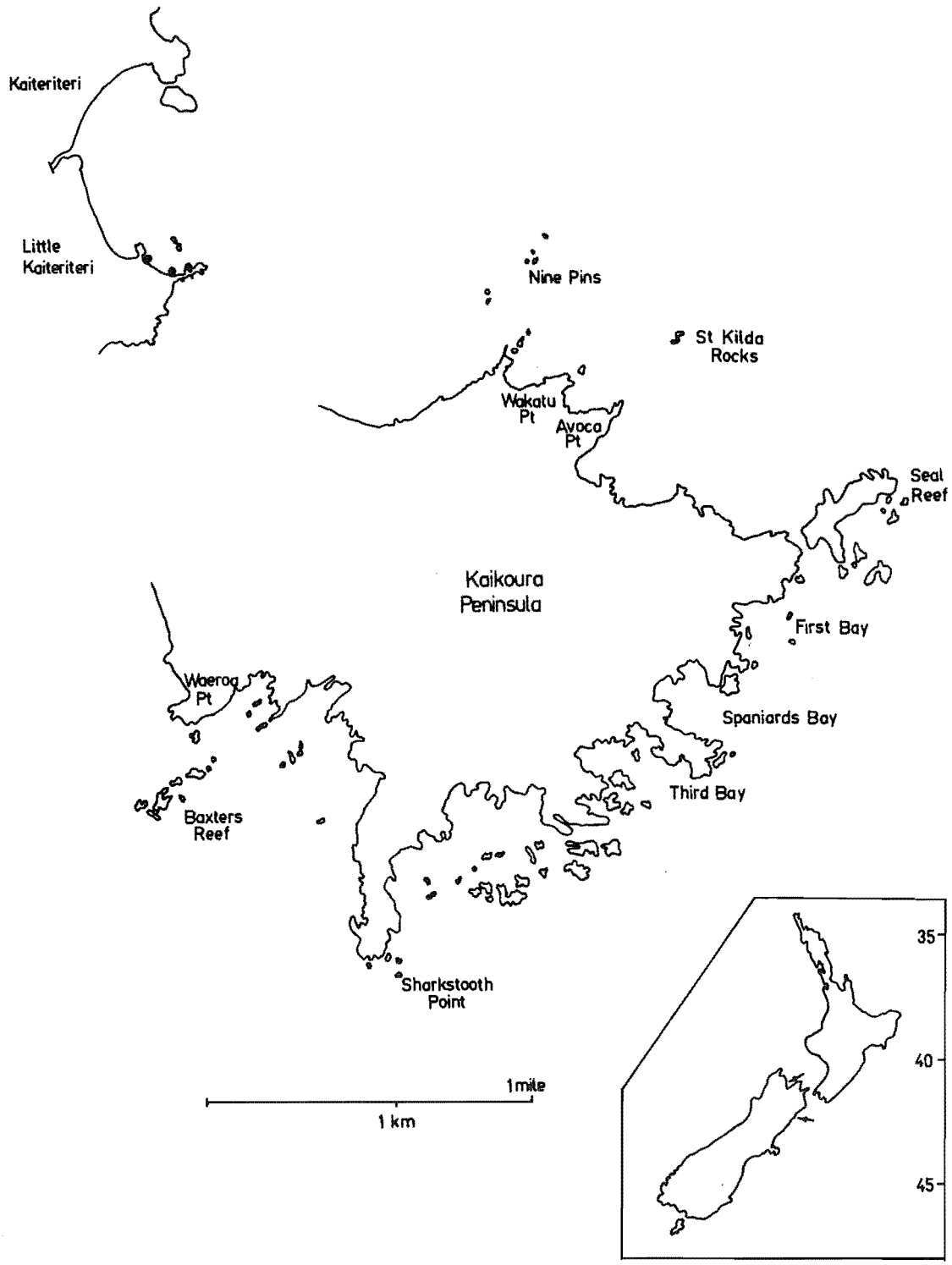

Kaiteriteri
Little Kaiteriteri
Nine Pins
St Kilda Rocks
Wakatu Pt
Avoca Pt
Seal Reef
Kaikoura Peninsula
First Bay
Waeroa Pt
Spaniards Bay
Third Bay
Baxters Reef
Sharkstooth Point
1 mile
1 km
35
40
45

Figure 1

Major study areas. Little Kaiteriteri, Kaiteriteri to the north and Kaikoura Peninsula to the south of the South Island (see arrows in inset). Traced from Lands and Survey Department aerial photographs.

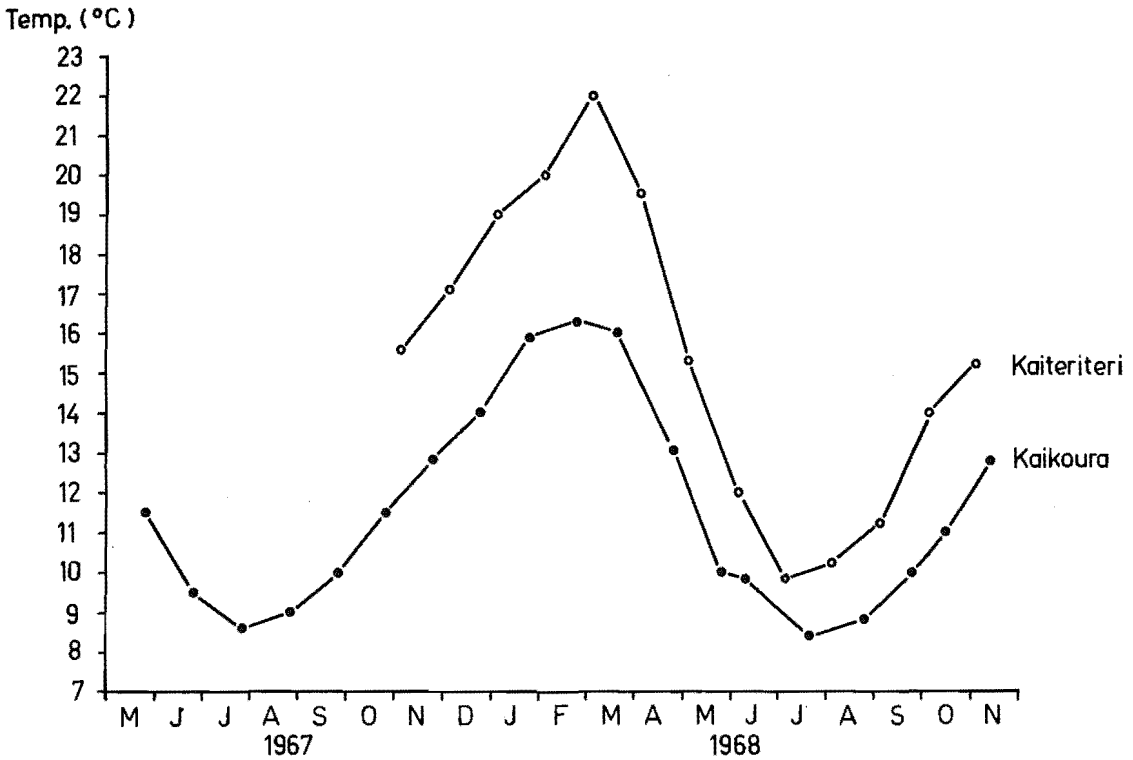

Temp. (°C)
23
22
21
20
19
18
17
16
15
14
13
12
11
10
9
8
7
M J J A S O N D J F M A M J J A S O N
1967
1968
Kaiteriteri
Kaikoura

Figure 2

Sea temperatures at Kaikoura and Kaiteriteri, 1967 - '68. Based mainly on single recordings each month at Seal Reef and Little Kaiteriteri.

at Kaiteriteri (Fig. 2) and salinities are probably lower.

(b) Algal abundance and diversity. Kaikoura is rich in marine species, a mixture of northern, southern and universal New Zealand species being present (Rasmussen, 1965). Subtidal rocks are rarely bare and Rasmussen recorded nine species of Chlorophyta, 90 of Rhodophyta and 39 of Phaeophyta from the intertidal zone and from drift in the area. In contrast, Kaiteriteri shows a marked paucity of marine algae. Except for a narrow band of the brown alga Carpophyllum maschalocarpum just below low tidal level, subtidal rocks are typically bare of macroscopic algae. Intertidally Hormosira banksii, Corallina and, seasonally, Scytosiphon lomentaria are only locally abundant. This contrast in algal abundance is shown in Frontispiece and Plates 1 and 3.

(c) Exposure to wave action. Kaikoura on the open coast of the South Island, is subjected to much greater wave action than Kaiteriteri. Depths greater than 10m are often subjected to strong wave surge at Kaikoura but rarely, if at all, at Kaiteriteri.

Aspects of the general biology selected for study were: occurrence and general habits; morphological variation; abundance; vertical and horizontal patterns of distribution; feeding habits; associates and, predation. More specific population studies investigated dispersal, reproduction, individual age determination, age structure and growth. The study aimed to compare the biology and population ecology of populations living in different environments and investigate reasons for the observed differences, particularly in size compositions.

1.2 Systematic Position

The systematic position of Evechinus chloroticus, as given by Mortensen (1943) is:

ORDER CAMARODONTA
Suborder Echinina
Family Echinometridae
Evechinus chloroticus (Valenciennes 1846)

McRae (1959) examined the familial status of Evechinus and suggested inclusion in either the Strongylocentrotidae as advocated by Clark (1925) or the Echinometridae as suggested by Mortensen (1943), but not the closely related Echinidae.

The present study did not examine the higher systematics since the specific status is well established.

1.3 Geographical Distribution

No systematic study of the geographical distribution of Evechinus was made during this study. The urchin is, however, endemic to the New Zealand region, ranging the whole of the New Zealand mainland and nearby islands (Mortensen, 1943; Pawson, 1961). It is also recorded from the Kermadecs (Fell, 1953; Pawson, 1961, 1965a; McKnight, 1968), Snares (Pawson, 1965b) and Chatham (Fell, 1960) Islands.

The Kermadecs records seem doubtful. Pawson (1961) recorded E. chloroticus from the Kermadecs on the basis of a personal communication with Professor H. B. Fell (D. L. Pawson, pers. comm.). After describing echinozoans collected by the 1962 Tui expedition north of New Zealand Pawson (1965a) again listed Evechinus from the Kermadecs. Three species of urchins were collected during shore sampling by the Tui expedition at the Kermadecs but Evechinus was not seen (M. C. Miller, pers. comm.). McKnight (1968) recorded Evechinus from the Kermadecs but this was based on Pawson's (1961, 1965a) earlier records (D. G. McKnight, pers. comm.).

It is now Fell's (pers. comm.) opinion that "there is no very precise statement as to exactly when and where in the Kermadecs Evechinus was supposed to have been found and my feeling is that a mistake may have occurred ... and that a myth developed simply by people repeating it to each other." It is possible that the Kermadecs record stemmed from Farquhar (1898) who stated that "Evechinus ... ranges northwards to Fiji," but in a later paper (1926) he stated that the genus is "monotypic and endemic" to New

Zealand. Further, Benham (1910) in a list of littoral echinoderms known from the Kermadecs, did not include E. chloroticus. Mortensen (1943) did not include the Kermadecs in the distribution range.

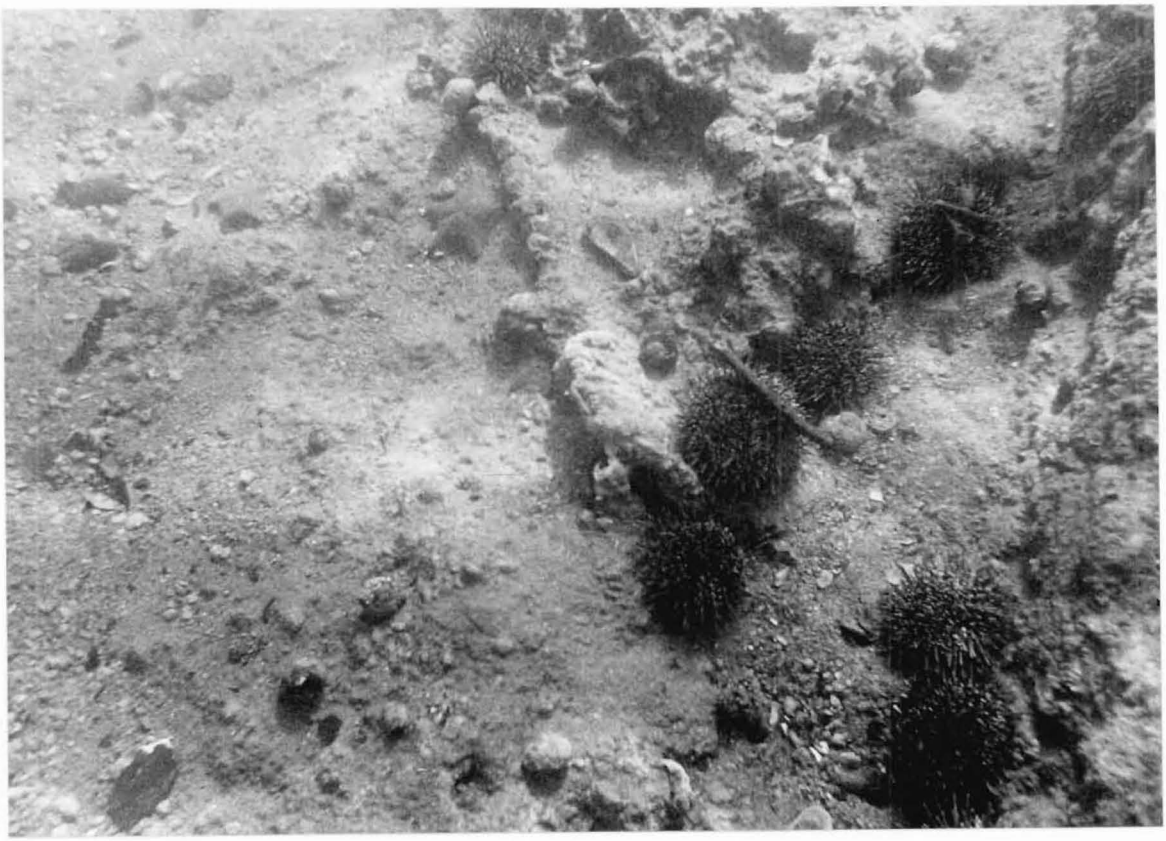
Thus it would appear best to eliminate the Kermadec Islands from the distribution range of Evechinus as is presently known.

Plate 1

Aggregation of Evechinus in a typical habitat in 7m depth at Third Bay, Kaikoura, 9 November 1967. Note extensive covering of algal debris. Urchins about 11cm diameter. Photo, T. G. Dix.

Plate 2

Depressions formed by Evechinus in siltstone (mudstone) rock in 9m depth at St Kilda Rocks, Kaikoura, 7 August 1968. Width of depressions about 15cm.
Photo, T. G. Dix.



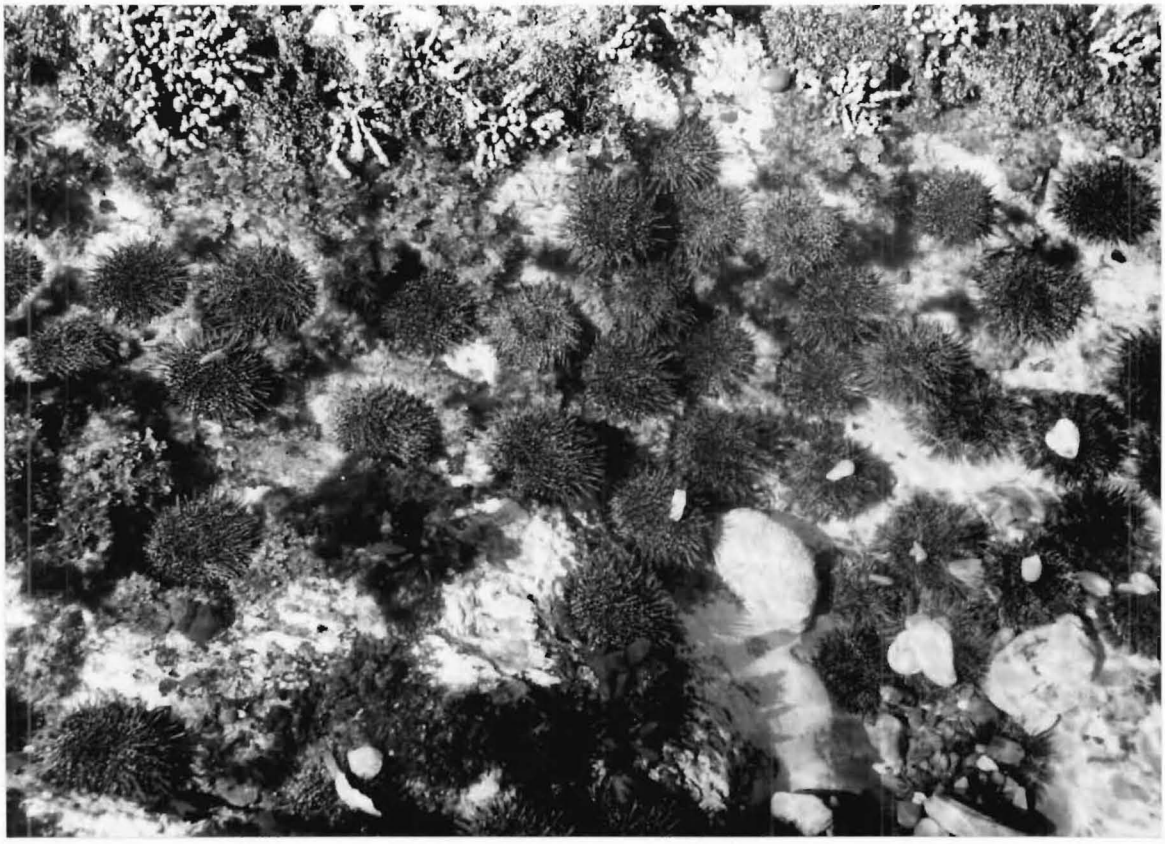


Plate 3

Evechinus in a typical habitat at 3m depth, Kaiteriteri, 7 August 1968. Urchins about 5cm diameter.
Photo, T. G. Dix.

Plate 4

Intertidal aggregation of Evechinus in a pool near mid-tidal level, D'Urville Island (Marlborough Sounds), August 1960.
Photo, G. A. Knox.

2. ECOLOGICAL DISTRIBUTION

2.1 Occurrence

Evechinus is typically a rocky bottom dweller (Fell, 1952; Morton and Miller, 1968; personal observations) but it may be found on other substrates. At Kaikoura it was found to occur almost entirely on hard stable substrates and it was never found on bare, unstable coarse sand. While mainly restricted to rocky bottom at Kaiteriteri and parts of Queen Charlotte Sound, Evechinus was often found on shelly sand and mud at the latter and sometimes found on bare sand and mud in both these localities; these soft bottoms are, however, much more stable than the wave-washed soft bottoms of Kaikoura. Graham (1962 and pers. comm.) recorded Evechinus from muddy shell-sand offshore at Oamaru and Maxwell (1957) noted its occurrence in the Wellington region "on sand bottom ... stone and gravel bottom ... rock bottom [and] in masses of seaweed."

Very young Evechinus (less than 1cm diameter) were never found in quantity although those seen were generally attached to the undersurfaces of both intertidal and subtidal rocks. F. M. Climo (pers. comm.) stated that he obtained fair numbers of very small Evechinus in gritty shell and sand bottom in Golden Bay, Nelson. Although extensive searching was not carried out, a few were found in similar habitats near the bases of rocks at Kaikoura.

Juveniles (about 1 to 4 cm diameter) are generally inconspicuous and found both intertidally and subtidally in two habitats: under rocks, particularly those resting on pebbles, or tucked in small crevices and depressions in rocks where they are generally extensively covered with debris.

Subtidal adults are generally conspicuous, often being without cover or partially covered on the tops and sides of rocks or on flat bottoms (Frontispiece, Plates 1 and 3). Intertidally, however, they are typically less conspicuous although this is not always so (Plate 4). In the sheltered pools of Kaiteriteri they

are generally partially or completely covered in dead mussel shells (Mytilus edulis and Perna canaliculus) or they are under ledges. At Kaikoura, where few sheltered pools exist and mussel shell or pebble debris is uncommon, adults are generally found extensively covered with algae under ledges or wedged in crevices.

Hyman (1955) citing part of Farquhar (1898) regarded Evechinus as a burrowing echinoid but as found by Farquhar this habit is not universal.

While the habit may be related to the movement patterns of the urchin (Section 9.3d) the extent of burrowing probably also depends on the hardness of the substrate. Of other urchins Otter (1932) suggested that "coarse textured rocks can be burrowed into quicker than rocks of fine texture ... but much depends on their degree of disintegration." Evans (1968) found that burrow shape in the rock boring clam, Penitella penita, was mainly influenced by rock hardness. Table 1 suggests that the extent of burrowing in Evechinus is related to rock hardness, deeper burrows being found in softer and/or easily disintegrated rock. It is notable that limpet and chiton scars, common on mudstones and limestones at Kaikoura, are rarely observed on graywacke. Further, burrowing molluscs and polychaetes are rare at Whareriki but common at Kahurangi (F. M. Climo, pers. comm.).

2.2 Abundance

Evechinus is often very abundant ("... is found in enormous numbers..." Young, 1929). Individuals in dense aggregations often touch or nearly touch each other (Frontispiece, Plates 1, 2 and 4), although marked density changes occur in small areas (Section 2.4). Densities recorded in the Sharks Tooth Point, Snake Point and Wakatu Point transects (Figs. 3 and 4) and from a transect at Kaiteriteri are summarised in Table 2.

Table 1 : Extent of burrowing in Evechinus populations

	Locality*	Rock type	Hardness	Burrows	Reference
1.	Kaikoura	Limestone	Fairly soft	Shallow depressions+	Dix (pers.obs.)
		Mudstone	Soft	Shallow depressions+	
		Graywacke	Hard	No depressions	
2.	Kaiteriteri	Granite	Hard, but crumbly	No depressions	Dix (pers.obs.)
3.	Kahurangi Point	Mudstone	Soft	Fairly deep depressions	(Mr F.M. Climo pers.comm.)
4.	Whaririki	Conglomerate	Hard	No depressions	" " "
5.	Mahi Peninsula	Mudstones, sandstones	Soft	Fairly deep depressions	(Dr R. McLean pers.comm.)
6.	Open Bay Island	Indurated calcareous mudstone	Hard but disintegrates in water	Fairly deep depressions	(Prof. G.A. Knox pers.comm.)

* Localities: 1 and 2, various intertidal and subtidal areas;
3 and 4, intertidal pools in north west Nelson;
5, intertidal pools and channels in Gisborne;
6, intertidal pools and channels in Westland.

+ See Plate 2.

Table 2 : Density of Evechinus recorded from transects at Sharks Tooth Point and Wakatu Point, Kaikoura; Snake Point, Queen Charlotte Sound, and Kaiteriteri.

Locality	Density (/m^2)	
	Mean	Range
Sharks Tooth	6.05	0 - 25
Wakatu Point	2.65	0 - 50
Snake Point	2.24	0 - 7
Kaiteriteri*	3.5	-

* from a 30m x 2m strip (not figured)

2.3 Vertical distribution

Mortensen (1943) stated that "Evechinus is eminently a littoral form, not known from deeper water than c. 20m.", while Morton and Miller (1968) observed that it "is secretly low tidal in the Hauraki Gulf, but on open shores reaches ... the midlittoral ... They are more numerous subtidally." The present section elaborates these statements in terms of intertidal and subtidal vertical distribution.

2.3a Intertidal vertical distribution

No systematic study of the intertidal distribution of Evechinus was made during this investigation but observations made during many collecting trips at Kaikoura and Kaiteriteri suggested the following generalisations: Evechinus is rarely found in situations where it is exposed to the air although a few are sometimes found out of water near LWST level during extreme low spring tides at Kaiteriteri. It is more abundant intertidally at Kaiteriteri (and also parts of the Marlborough Sounds; Plate 4) than at Kaikoura. Over 300 could be collected by the author during one tide at Kaiteriteri but fewer than 20 could generally

be collected in a similar time at Kaikoura. Further, Evechinus extends over a greater intertidal range at Kaiteriteri. Here it is often found in pools in the midlittoral (barnacle) zone while at Kaikoura it is almost entirely restricted to very low level pools and channels.

Evechinus extends over most of the intertidal zone at Leigh, Hauraki Gulf (R. T. Paine, pers. comm.) and it was also noted in the midlittoral zone at Wellington by Oliver (1923). G. A. Knox (pers. comm.) mentioned that Evechinus is restricted to the subtidal and very deep intertidal pools at Banks Peninsula, and is almost exclusively subtidal on Stewart Island and on the Snares Islands. Although he mentioned abundant intertidal populations extending to the midlittoral zone at Open Bay Island, Jacksons Bay, Westland, a general pattern of greater intertidal abundance and range northwards is evident. Bennett and Pope (1953) also found a similar pattern with the urchin Heliocidaris erythrogramma in Australia; this urchin is common intertidally in New South Wales but is restricted to subtidal levels in Victoria. Some New Zealand organisms (e.g. Perna canaliculus; W. J. Ballantine, pers. comm.) show the reverse pattern and it is Ballantine's opinion that both patterns may be related to the temperature tolerances of the organisms.

2.3b Subtidal vertical distribution

A general study of subtidal vertical distribution was made, by diving observations and by transects, at Kaikoura, Kaiteriteri and Queen Charlotte Sound.

Numbers of Evechinus within one metre of each side of a transect line were observed by two divers within five metre intervals in transects at Snake Point, Queen Charlotte Sound (February 1968) and Sharks Tooth Point, Kaikoura (November 1968). Depths at each interval were noted and bottom profiles were later constructed. Major features of the substrate and of algal composition and abundance were also noted. Mean numbers of Evechinus per five square metres and bottom profiles are shown in

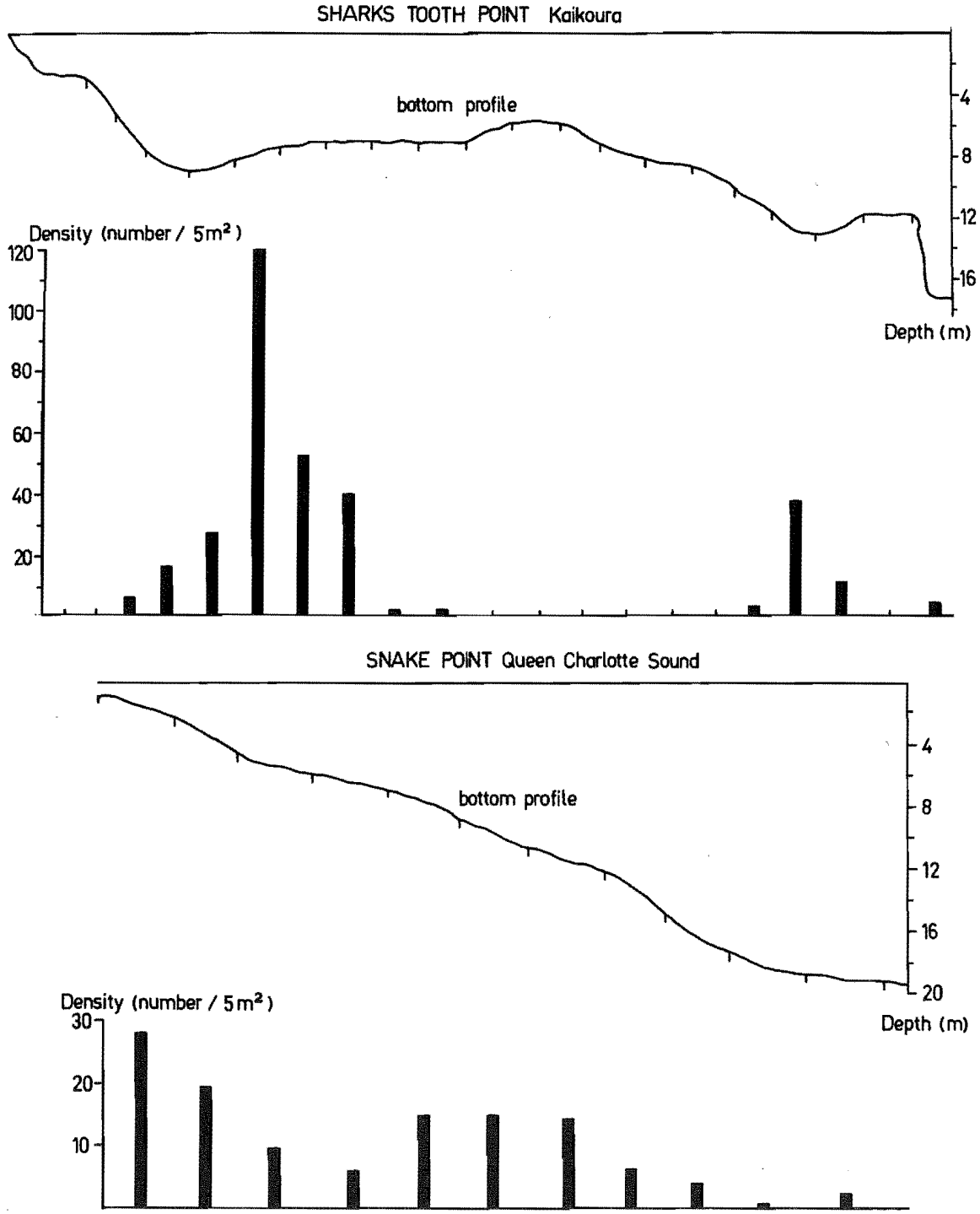

SHARKS TOOTH POINT Kaikoura
bottom profile
4
8
12
16
Depth (m)
Density (number / 5m²)
120
100
80
60
40
20
SNAKE POINT Queen Charlotte Sound
bottom profile
4
8
12
16
20
Depth (m)
Density (number / 5m²)
30
20
10

Figure 3

Subtidal vertical distribution of Evechinus and bottom profiles at Sharks Tooth Point (November 1968) and Snake Point (February 1968).

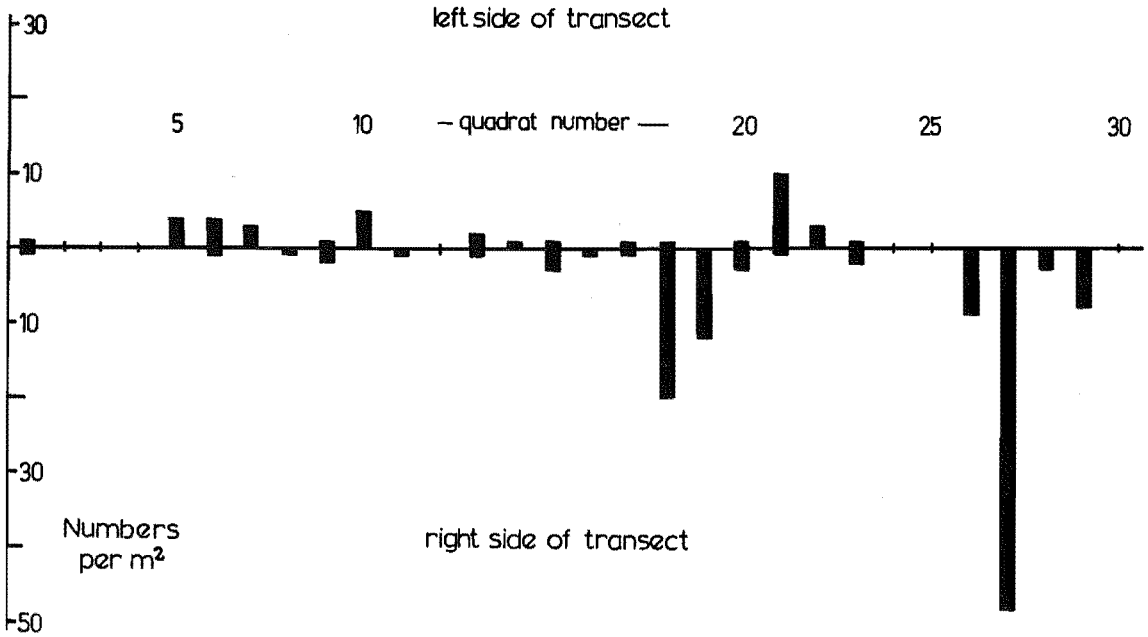

left side of transect
30
5
10
– quadrat number —
20
25
30
10
10
30
Numbers
per m²
right side of transect
50

Figure 4

Number of Evechinus in 60, m^2 quadrat samples in 2 - 4m depth at Wakatu Point, July 1967.

Fig. 3.

At Sharks Tooth Point, Evechinus was locally very abundant at a depth of 8m in a rocky area dominated by a luxuriant growth of mixed brown algae. Less dense concentrations also occurred at a depth of 13m where brown algae were also very abundant. Just below this the bottom dropped steeply to a depth of 17m and then flattened. This area, with large stones and rocks, contrasted with that above in that smaller red algae were dominant and brown algae were sparse. Evechinus was very scattered at this depth.

This vertical distribution pattern of dense patches of Evechinus in the subtidal zone dominated by brown algae is considered typical for Kaikoura. However, some variations occur; firstly, the centres of Evechinus abundance shift over most of the brown algal zone. In some areas (e.g. Wakatu Point) a centre of abundance is found in depths of 2 - 3m while in others (e.g. parts of Seal Reef) it may be at 14 - 15m. In other areas (e.g. St Kilda Rocks) high density Evechinus patches may occur at several depths within the brown algal zone. Secondly, observations to a depth of 20m at the tip of Seal Reef and also at parts of Sharks Tooth Point showed Evechinus to be very abundant in a narrow band at 18m in the area immediately below the zone of brown algal dominance; this area is comparatively barren but is dominated by smaller red algae.

At Snake Point, Evechinus tended to be more evenly spread although considerable concentrations occurred on rocks and stones in 2 - 4m immediately below a distinct band of the brown alga Carpophyllum maschalocarpum. Few were present on the barren large stones at 6m but densities showed some increase at 8 - 12m where the substrate changed to areas of soft shell-littered bottom with conspicuous and common mounds of a serpulid worm (species not known). A spindly red alga became common at 10m and extended to 15m. Below the serpulid and red algal band the bottom consisted of muddy shell sand and here Evechinus became very scattered. Although not shown in Fig. 3, scattered Evechinus occurred on this

bottom to depths of at least 28m. Observations at other parts of Queen Charlotte Sound (Resolution Bay, Blumine Island, Cockle Cove) showed the above pattern to be repeated although in some areas (e.g. Ruakaka) where the conspicuous band of Carpophyllum was absent, Evechinus did not show a marked rise in density in shallow water.

Although transects to define depth distribution were not done at Kaiteriteri, Evechinus was concentrated on bare rocks in 2 - 4m immediately below a Carpophyllum band. Below this the bottom became sandy and sparsely shell littered and then muddy and extensively shell littered; Evechinus was very sparse on these bottoms. Depths greater than 9m were not observed at Kaiteriteri since these did not occur close inshore.

In all areas observed, Evechinus showed peaks of abundance in the shallow subtidal zone. In the northern South Island areas these were generally not far below ELWS tide level while at Kaikoura they were typically deeper. Possible factors causing these differences could include (a) wave action; (b) extent of algal occurrence; (c) substrate.

Kaiteriteri and Queen Charlotte Sounds are very sheltered from wave action while most areas at Kaikoura are very exposed. Pérès (1967) related a vertical subdivision of the subtidal benthic zone on hard substrates to wave action; an upper layer subjected to multidirectional stirring and a lower layer of unidirectional motion were separated by a critical level whose depth was directly proportional to wave amplitude. Morgans (1959) also indicated that wave turbulence affected the distribution and occurrence of shallow subtidal organisms. Field observations suggest that Evechinus is generally intolerant of wave action and it is possible that the lower centres of abundance at Kaikoura relate to this.

The facts that almost all macroscopic algae is in shallow water at Kaiteriteri and, to a lesser extent, parts of Queen Charlotte Sound and that Evechinus is predominantly algivorous

(Section 4.4) may further serve to raise centres of abundance in these areas.

Abundance may also be restricted in deeper water in the northern South Island areas since Evechinus primarily lives on hard substrates and since these give way to soft substrates in shallower water than at Kaikoura.

The lower limits to distribution were not ascertained in this study. Evechinus was found to depths of 28m in Queen Charlotte Sound and although it was present in small numbers only at this depth, it may have occurred deeper. Diving to 26m at several parts of the Kaikoura Peninsula indicated that Evechinus was rare below 18m although, again, it may go deeper. D. J. Ingram (pers. comm.) who has dived extensively over rocky areas in the Hauraki Gulf to depths of 43m and who has systematically recorded observations on Evechinus abundance, never saw any aggregations below 15m and has found them uncommon below 12m; they were virtually absent below 15m. On a recent dive to 35m at Kapiti Island (Wellington), however, Ingram found Evechinus to be common above 28m on a boulder bottom with little macroscopic algae. J. Graham (pers. comm.) "obtained small numbers quite often but certainly not every time" he commercially trawled in an area about 8 miles offshore near Oamaru. This area, beyond a large inshore bed of Macrocystis pyrifera, extended from 27m to 55m and consisted of muddy shell sand, the shell fragments being encrusted with bryozoans and often being bound together by mytilids and polychaetes. No Evechinus were obtained below this depth (Graham, 1962).

2.4 Horizontal distribution

Evechinus is rarely evenly distributed over extensive areas; instead, isolated clumps or aggregations, often of high density (Section 2.2) are typical. Such clumping occurs at two levels. Firstly, populations within a given geographical area are generally separated by fairly extensive areas of low density and, secondly, clumping occurs within these populations. Super-imposed dispersion

patterns have also been observed by Buchanan (1967) in the ophiuroid Amphiura filiformis, the spatangoid Echinocardium cordatum and the holothurian Cucumaria elongata.

The sizes of Evechinus population clumps are hard to estimate but most probably contain from several to many thousand urchins. Infra-population clumps vary from about 20 to 500 urchins.

Factors influencing the formation of population clumps were not specifically studied. In some cases, however, populations on rocky areas (e.g. St Kilda Rocks) are separated from others (e.g. Seal Reef) by extensive areas of sand which are unsuitable for urchin colonisation. In other cases low density areas are apparently similar to nearby high density areas (e.g. at parts of Seal Reef and Sharks Tooth Point). It is possible that these populations result from localised settlement and/or survival of larval forms since Cassie (1963) has indicated that plankton is often over-dispersed.

2.4a Infra-population dispersion

Infra-population clumping is evident in the Sharks Tooth Point and Wakatu Point transects (Figs. 3 and 4) and also in Frontispiece and Plate 1. Further, the 60, m^2 quadrats from Wakatu Point gave a variance ratio test with $P < 0.005$. Such clumping has also been recorded for the echinoids, Diadema antillarum (Randall, Shroeder and Stark, 1964), Lytechinus variegatus (Moore et al., 1963a), and Psammechinus miliaris (Larsson, 1968). It is of common occurrence in echinoderms (Reese, 1966).

Infra-population clumps of Evechinus were observable throughout the year and thus did not represent seasonal spawning aggregations (c.f. Tennent, 1910).

Factors involved in infra-population clumping of Kaikoura Evechinus were experimentally investigated. In his review on "The complex behaviour of echinoderms" Reese (1966) suggested that it is a 'moot question' as to whether such clumping results from interaction between individuals or whether clumps are simply a result of individual reaction to the physical environment. The

occurrence of Evechinus clumps on some rocks but not on similar neighbouring rocks at Kaikoura suggested that aggregations of this species might result from individual interactions. To ascertain whether individuals of Evechinus might be chemically attracted a series of Y-maze experiments was performed. A stationary animal was placed behind a partition in one arm of a maze through which water flowed continuously at a slow rate. A second, mobile individual was placed in the tail of the Y; responses were recorded as positive if the mobile individual moved up to the partition containing the stationary animal, negative if to the other. After about every three responses the stationary animal was moved to the opposite arm of the maze to remove possible bias and after the end of each experiment the animals were sexed. Results of these experiments using 44 Evechinus over a period of six months (Table 3) indicate that the ratios of total negative to total positive responses show a highly significant departure from 1:1 ($\chi^2 = 26.51$, $P < 0.001$), suggesting that chemical attraction may play a significant part in the behaviour of aggregating in Evechinus.

Table 3 : Y-maze responses of Evechinus at Kaikoura

	Positive	Negative
Heterosexual	97	50
Homosexual	40	14
Total	137	64

It appears that no significant difference exists between homosexual and heterosexual response ratios ($\chi^2 = 1.19$, $P = 0.3$) suggesting that attraction between individuals is independent of sex. This suggestion is strengthened by field observations. Relative positions of 161 individuals (72 females and 89 males) from five different aggregations were recorded in the field; for each individual its sex and that of its nearest neighbour were

noted. The numbers of pairs of females nearest females, males nearest males and females nearest males thus observed were tested against expected numbers under the hypothesis that 'there is no preferred association between two individuals in terms of sex' or that 'the sexes are randomly distributed with respect to each other'. Under this hypothesis, if p is the proportion of females in a sample and q the proportion of males, then the proportion of female nearest female pairs = p^2, male nearest male pairs = q^2 and female nearest male pairs = 2pq. Results show that there is no cause to reject the hypothesis in any of the five samples (Table 4).

Table 4 : Pairing of individuals in Evechinus at Kaikoura

Sample	♀♀	♂♂	Nearest neighbour pairs ♀-♀	♀-♂	♂-♂	χ^2	P
A	15	10	6	16	3	1.50	0.4
B	13	14	8	14	5	1.12	0.5
C	13	19	5	14	13	0.54	0.7
D	14	23	5	20	12	0.73	0.6
E	17	23	9	18	13	0.58	0.7

Thus aggregations appear to consist of individuals which are chemically attracted to each other independent of sex, an approximately equal sex ratio (Section 10.3c) and chance ensuring that enough males and females are present in each clump to ensure reproductive success. If mass spawning occurs in nature, it is unlikely that the reproductive success of closely packed aggregations showing random distribution of sexes would be any less than that of aggregations showing heterosexual pairing.

Although choice chamber experiments were not conducted with Kaiteriteri Evechinus, it is considered possible that infrapopulation clumping is here more dependent on individual response

to environmental factors than at Kaikoura. Small aggregations occupying bare areas were frequently found clustered around drifting Carpophyllum at Kaiteriteri (and also parts of Queen Charlotte Sound) and these gave the impression that individuals had converged on the Carpophyllum. Algae, both drifting and attached, is far more abundant at Kaikoura and it is possible that individual attraction of Kaikoura Evechinus to this is less important.

Aggregations in intertidal pools (Plate 4) might also result from individual response to the presence of permanent water.

2.5 Summary

Evechinus is typically a rocky bottom dweller with adults, juveniles and very small individuals occupying different habitats. Adults may make excavations into rock, the depth of the excavations possibly depending on rock hardness.

The urchin is often very abundant, densities sometimes exceeding 50 adults per m^2.

Evechinus is chiefly a shallow (<12m) subtidal species although considerable intertidal populations are found in some areas, particularly northwards. The lower limit to distribution is not known but is possibly about 50m.

A super-imposed dispersion pattern of population and infra-population clumping is typical. Field observations and choice chamber experiments at Kaikoura suggest that chemical attraction between individuals plays a significant part in the behaviour of infra-population aggregating and that attraction is independent of sex.

3. MORPHOLOGICAL VARIATION

3.1 Introduction

Many workers have recognised the existence of morphological variation in echinoids, much of the literature on this topic being listed in the introduction of Lohavanijaya (1965) and in Swan (1966).

Variation investigated in the present study concerns test shape (ratio of test height to diameter), spination and test thickness. Populations of Evechinus inhabiting environments differing in several respects were sampled in the hope that causal relationships might be suggested.

3.2 Materials and methods

Collections were made by diving at Kaikoura and Little Kaiteriteri, Kaiteriteri. Three localities separated by less than a mile were sampled at Kaikoura: Wakatu Point, a generally surf-washed area 1 - 3m in depth; St Kilda Rocks, in depths of 8 - 12m, not exposed to surf but to strong surge during very rough seas, and Seal Reef, in 8 - 14m, an area similar to St Kilda Rocks. Little Kaiteriteri was shallow (3 - 5m) but sheltered, rarely if ever being exposed to surf or even strong wave surge. In contrast to the Kaikoura localities, macroscopic algae were sparse (Section 1.1).

The ratio of test height to test diameter, measured to the nearest mm with the apparatus described in Appendix 1, was used to describe test shape. Over the size ranges studied, this ratio changed little and mean values could be used to compare different populations. Test thickness was measured with vernier calipers on the cut edge of an interambulacral plate within 1cm of the centre of the periproct and was expressed relative to diameter.

3.3 Results and discussion

Moore (1935) for Echinus esculentus and McPherson (1965) for Tripneustes ventricosus found flatter tests in populations subjected

to wave exposure than in those of calm areas. As an extension of Thompson's (1917) ideas they suggested that growth of tests in areas of heavy wave action would be under greater stress from the tube feet used for attachment than the growth in relatively calm areas.

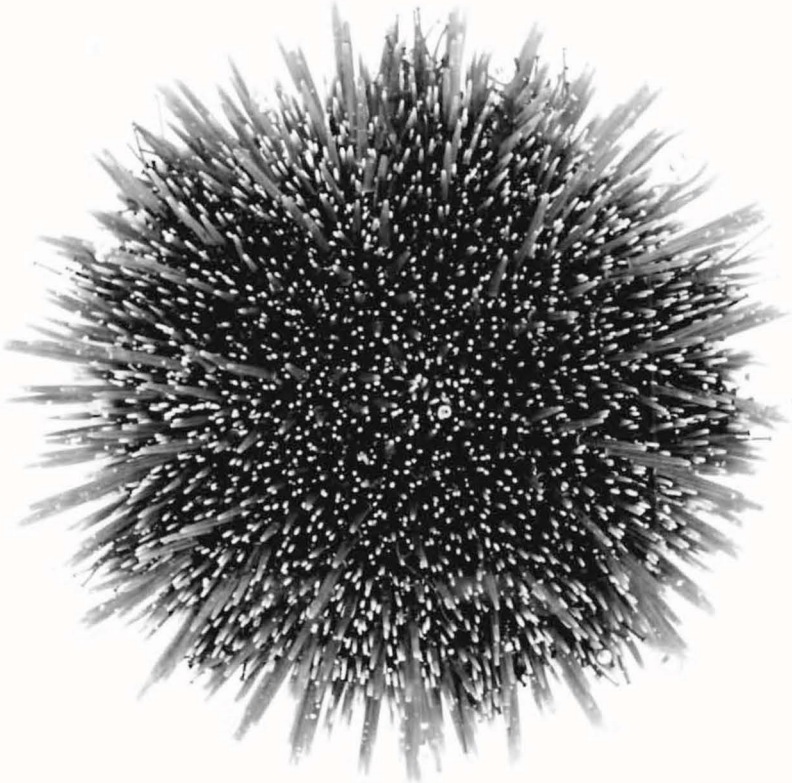
Although Evechinus was more firmly attached to the substrate at Wakatu Point, the most exposed of the sampling areas, observations showed that attachment was almost entirely maintained by the oral surface tube feet. Thus the rest of the test is free to grow apparently uninfluenced by stresses exerted by attached tube feet. Therefore, there is no reason to postulate flatter tests in more firmly attached urchins. Significantly, t-test analyses of mean ratios of height to diameter for each Evechinus population sampled showed there was no significant difference in test shape (Table 5). Further, McPherson (1968) found that Eucidaris tribuloides tended to be flatter in calmer than in rougher water.

Table 5 : Test shape in different populations of Evechinus

Locality	Exposure	Mean h/d*	s	N
Wakatu Point	Surf washed	0.56	0.08	75
St Kilda Rocks	Surge only	0.54	0.04	43
Seal Reef	Surge only	0.57	0.04	50
Kaiteriteri	Sheltered	0.56	0.03	50

* h = test height; d = test diameter

The spination pattern does, however, vary from locality to locality. The differences are readily apparent (Plates 5 and 6). Wakatu Point urchins have short, thick spines with rounded tips, Seal Reef and St Kilda Rocks urchins are intermediate while Kaiteriteri urchins have relatively long thin spines with sharp tips. Breakage and regeneration, observed in intact and longitudinally sectioned spines, are typical of Wakatu Point specimens



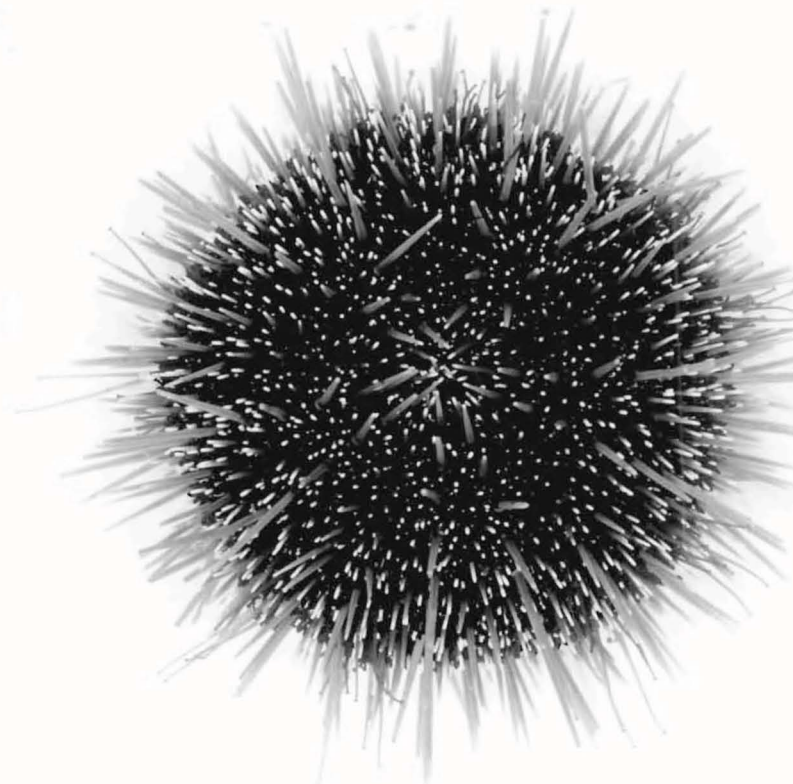


Plate 5

Aboral view of Evechinus from Wakatu Point, Kaikoura. Note short, blunt, stout spines. Urchin diameter 8.5 cm. Photo, B. M. Dukes.

Plate 6

Aboral view of Evechinus from Kaiteriteri. Note long, pointed, fine spines. Urchin diameter 4.8 cm. Photo, B. M. Dukes.

but are less common in the other localities. Breakage, which possibly results from bombardment by surf-washed debris, has also been attributed to wave action in Heliocidaris erythrogramma (G. P. Moore, 1966) and Strongylocentrotus purpuratus (Ebert, 1968).

Least square regressions of test thickness on test diameter for each locality (Table 6) are plotted in Fig. 5. For simplicity individual points are plotted only for Wakatu Point and Kaiteriteri, but all regressions were significant.

Table 6 : Least square regression equations of test thickness (t) on test diameter (d) for different populations of Evechinus

Locality	N	Equation	Significance P
Wakatu Point	40	$t = 0.12d + 1.02$	<0.001
St Kilda Rocks	50	$t = 0.10d + 1.09$	<0.001
Seal Reef	42	$t = 0.08d + 1.35$	$0.01 > P > 0.005$
Kaiteriteri	55	$t = 0.12d + 0.75$	<0.001

Unfortunately, due to restricted size ranges in some localities, all comparisons could not be made with urchins of similar size but since the relationship between test thickness and diameter was linear over the size ranges considered, comparisons seem justified. Evechinus tests are relatively thicker at all the Kaikoura localities than at Kaiteriteri (Fig. 5) and are relatively thicker at Wakatu Point than the deeper Kaikoura localities.

The major environmental differences between the four localities concern wave action, temperature and amount of algae present. Moore (1935) attributed differences in the test thickness of Echinus esculentus to differences in exposure to wave action but also suggested that diet might play a part. Giese (1967) suggested that the body wall index [weight of the body wall relative to the weight of the urchin] of Strongylocentrotus purpuratus "may be a

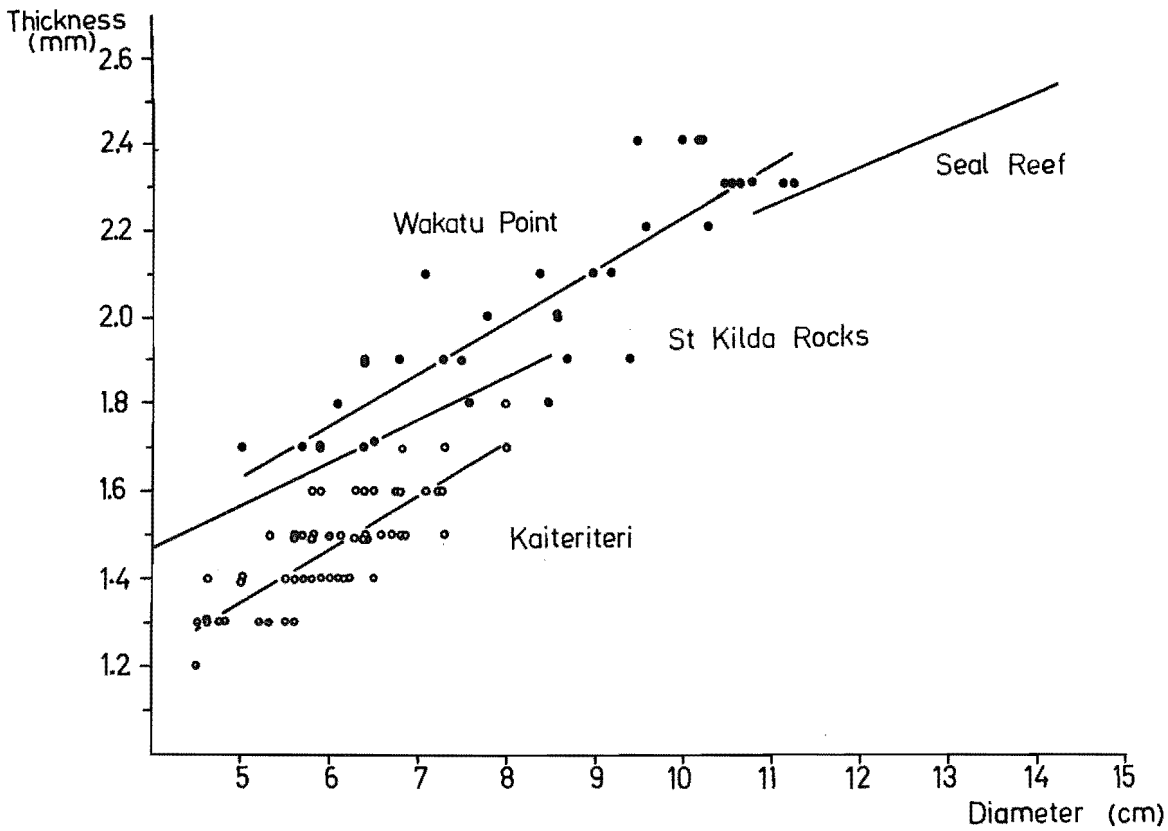

Thickness (mm)
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
5
6
7
8
9
10
11
12
13
14
15
Diameter (cm)
Seal Reef
Wakatu Point
St Kilda Rocks
Kaiteriteri

Figure 5

Least square regressions of test thickness on test diameter for four Evechinus populations. For simplicity points are plotted only for Wakatu Point and Kaiteriteri.

character of a specific population of the animals, probably related to nutrition and other stresses." Raup (1958) found tests of the sand dollar Dendraster excentricus to be relatively heavier in cold water than in warm water. Water temperatures are generally 2 - 5° C higher at Kaiteriteri than at Kaikoura (Fig. 2) and it is possible that this in some way might account for the observed differences in Evechinus test thickness.

Nutrition may also be significant, since experiments with fed and starved Evechinus showed that food quantity can influence test thickness. Samples of 40 Kaiteriteri urchins and 36 Kaikoura urchins were kept in running seawater trays at Kaikoura as described in Section 10.3a. After six months the mean relative test thicknesses [$\frac{\text{test thickness in mm}}{\text{test diameter in cm}}$] of fed urchins were significantly greater than those of starved specimens (Table 7).

Table 7 : Mean relative test thickness of fed and starved Evechinus after six months

Specimens	Fed	Starved	t	P
Kaikoura	0.37	0.34	4.37	< 0.001
Kaiteriteri	0.33	0.29	3.96	< 0.001

3.4 Summary

Spine length, thickness and sharpness and also test thickness vary among Evechinus populations at Wakatu Point, Seal Reef and St Kilda Rocks, Kaikoura and at Kaiteriteri. No significant differences in the ratios of test height to test diameter were found. Variations in spination are probably related to amounts of wave exposure while test thickness is at least in part related to nutrition.

4. FEEDING HABITS

4.1 Introduction

Reviews on the feeding habits of sea urchins are given by Harvey (1956), Hyman (1955), Moore (1966) and Reese (1966), the observations being summarised by Hyman's statement: "it appears that most urchins will eat almost anything, but some tend to a carnivorous, others to a herbivorous, diet, although in the lack of preferred items they will ingest the bottom material, and in fact act as general scavengers."

Recorded observations of the feeding habits of Evechinus chloroticus are sparse. Mortensen (1943) noted that "in the intestinal canal I have found bits of algae, particularly Corallina, and bryozoa ..." while McRae (1959) stated that "...in general it may be said that Evechinus chloroticus feeds on littoral seaweeds and their associated epifauna ... although the animal appears to exhibit little power of selection." Dromgoole (1964) recorded depredation of beds of the brown alga Ecklonia radiata by E. chloroticus and suggested that the urchin "consumes all associated species in the Ecklonia community except for ... Lithothamnia."

In the present work a comparative study of Evechinus at Kaikoura and Kaiteriteri was made to see if urchins living in different environments (Section 1.1) showed different feeding habits.

4.2 Methods

By using diving equipment the writer was able to examine the mouths of Evechinus in situ and note the presence and type or absence of food material. Mauzey, Birkeland and Dayton (1968) have made similar observations on the feeding behaviour of asteroids. Samples of 100 urchins at Kaiteriteri and two of 40 at Kaikoura were examined in February 1968; scattered observations were made at other times at these localities and also at Queen Charlotte Sound.

Gut contents of samples from Kaikoura and Kaiteriteri were also examined but it was found that the food was generally too finely divided to be identifiable; but these examinations gave a good indication of the amount of bottom material ingested.

Observations on materials eaten in laboratory tanks were also made.

4.3 Results

A broad classification of the types of food found in the teeth of specimens from Kaikoura and Kaiteriteri is shown in Table 8. Individuals considered to be browsing had either small pieces of rock, fine sand or fine debris in their teeth; some of the debris may have been microscopic algae or sessile animal material. Specimens with shell held to their mouths were probably also browsing.

Table 8 : Food observed in the mouths of Evechinus in their natural surroundings at Kaikoura and Kaiteriteri *

	Percentages with each type of food			
Food	$Kaikoura_1$	$Kaikoura_2$	Combined Kaikoura	Kaiteriteri
Brown algae	10.0	27.5	18.8	20.0
Red algae	60.0	12.5	36.3	1.0
Green algae	2.5	5.0	3.8	0.0
Browsed material	15.0	32.5	23.8	48.0
Shell	0.0	0.0	0.0	9.0
Leaf	0.0	0.0	0.0	1.0
Stick	0.0	0.0	0.0	1.0
None	12.5	22.5	17.5	20.0

* Kaikoura: 40 specimens examined on 16.2.68 and 40 on 27.2.68
Kaiteriteri: 100 specimens examined on 2.2.68.

A variety of both brown and red algae were utilised at Kaikoura. Brown algae included Carpophyllum maschalocarpum, Desmerestia firma, Ecklonia radiata, Halopteris spicigera, Landsburgia quercifolia, Lessonia variegata and Marginariella boryana while red algae included Corallina (branching and encrusting forms), Cladhymaenia oblongifolia, Lenormandia chauvinii, Plocamium costatum and at least five unidentified species. The green alga, Caulerpa brownii was also utilised. In contrast, only two brown algae were utilised as food at Kaiteriteri; mainly Carpophyllum maschalocarpum with some Hormosira banksii. Only one specimen was found feeding on a red alga (Corallina).

The habits further contrast in that a greater proportion browsed on the substrate at Kaiteriteri. Correlated with this, the guts of Evechinus from Kaiteriteri almost always had much more finely divided inorganic material in them than those from Kaikoura.

Additional field observations during 1967-1969 at the two localities suggested that the above results were typical, and observations at parts of Queen Charlotte Sound (February 1968) where the environment is similar to that of Kaiteriteri, showed 'Kaiteriteri type' feeding habits. Some were also found ingesting detritus from soft bottoms in Queen Charlotte Sound while eight specimens were found at Kaikoura feeding on parts of the cast exoskeletons of crustaceans (5 on Jasus edwardsii and 3 on Plagusia crapensis).

A wide variety of materials was consumed in the laboratory. These included macroscopic and microscopic algae, detritus, dead molluscs, houseflies and fish, wood from the sides of tanks and vinyl tags.

4.4 Discussion

As some confusion exists in the classification of echinoderm feeding habits (Reese, 1966) terms used in the present study will be defined. Algivores are those feeding on macroscopic algae, while browsers are those feeding on material scraped from hard substrates; this material may include microscopic algae, encrusting

animals and detritus. Algivore and browser are categories within the term "grazer" of Reese (1966).

The present field and laboratory observations, together with the comments of Mortensen (1943), McRae (1959) and Dromgoole (1964) indicate that while Evechinus may eat a wide variety of food, it is chiefly algivorous. But where macroscopic algae are scarce, as at Kaiteriteri, the populations predominantly browse material from rocks. Further support for this pattern of feeding lies in the observations on a single population of Evechinus at Sharks Tooth Point, Kaikoura, every three days for over a month (Section 10.3a). When drift algae were abundant, guts contained large quantities of algae. During calm weather, with little drift algae, more browsed material was consumed. As with Diadema antillarum "... the food habits reflect the availability of food in the habitat ..." (Randall, Shroeder and Stark, 1964). Leighton, Jones and North (1966) found also that Strongylocentrotus purpuratus were predominantly browsers in barren areas and in aquaria but where kelp was abundant they fed mainly on this. Ebert (1968) found larger amounts of calcium carbonate in the gut of this species in an area with less abundant macroscopic algae than in a nearby richly weeded area.

Whether Evechinus preferentially feeds on particular species of algae as was shown for Lytechinus anamesus, S. purpuratus and S. franciscanus (Leighton, 1966) and S. intermedius (Fuji, 1962) was not ascertained during the present study.

4.5 Summary

At Kaikoura, where macroscopic algae are diverse and abundant, Evechinus is almost exclusively algivorous, but at Kaiteriteri, where such algae are sparse, it predominantly browses material from the substrate.

5. ASSOCIATES

5.1 General

Many different animals have been found in association with echinoids (Hyman, 1955) but as stated by Davenport (1966) the precise nature of these associations is known in few cases.

Internal associates noted during the present study included a rhabdocoele (Syndesmis sp.), present in the gut of most specimens; it was also noted in Wellington Evechinus by McRae (1959) and the genus is recorded from other echinoids (Stunkard and Corliss, 1951). Various ciliates were found in the gut and gonad but none was identified.

Previous to the present study, a small copepod ("yet to be positively identified" McRae, 1959) was the only external associate recorded. Although this animal, regarded by McRae as an ecto-commensal, was not seen by the present author three animals were found in association: a shrimp, Nauticaris marionis (J.C. Yaldwyn det.); a sphaeromid isopod, Exosphaeroma sp.* (K.P. Jansen det.) and a clingfish, Dellichthys morelandi (J. Moreland det.).

Nauticaris marionis was infrequently found beneath subtidal Kaikoura Evechinus but because of its infrequent occurrence and also its recorded distribution and habits (Richardson and Yaldwyn, 1958) it is unlikely to be a close associate.

Exosphaeroma sp was commonly found sheltering beneath or living among the spines of subtidal Evechinus at Kaikoura and Kaiteriteri. Although it is not known for certain whether this isopod lives elsewhere, it was not recorded by K. P. Jansen (pers. comm.) during extensive collecting of shore sphaeromids at Kaikoura. This, together with the frequency of association, the cryptic colouration of the isopod and its habit of lying along the spines of Evechinus so that its white uropods match the white-tipped secondary spines, suggest that the isopod may be a true commensal.

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*This is to be described as Exosphaeroma evechinensis by Jansen (pers.comm.)

5.2 The clingfish Dellichthys morelandi

5.2a Introduction

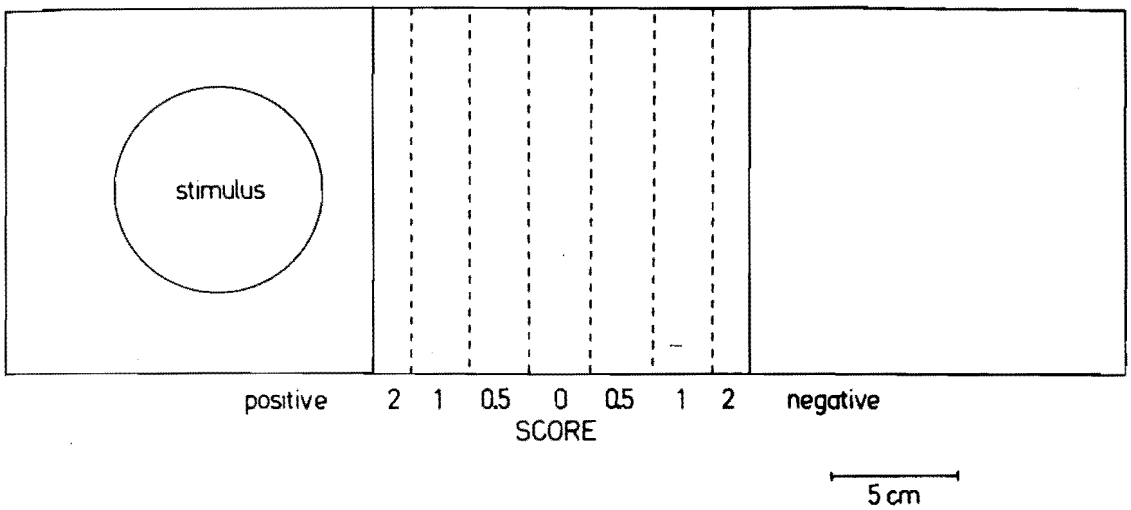
Fishes have been found living in external association with echinoids (Hyman, 1955; Pfaff, 1942). Pfaff described a clingfish, Diademichthys deversor, found amongst spines of the echinoid Diadema, noted that one specimen had tube feet in the gut and summarised the literature on echinoid-clingfish relationships. He pointed out that the precise nature of these relationships was not clear.

The present section suggests that Evechinus chloroticus provides shelter and food for the clingfish Dellichthys morelandi and that the latter recognises the echinoid visually. While diving for echinoid samples at Kaikoura the author noticed that adult and juvenile clingfish were very commonly found among the oral surface spines and attached to the substrate beneath the echinoid, and that when an urchin was lifted off the substratum any clingfish thus exposed darted rapidly under nearby, undisturbed urchins. It was then found that the clingfish were readily captured by removing Evechinus from rocks while holding a net containing several urchins nearby and that when an urchin was added to a laboratory tank containing clingfish they darted rapidly underneath. These observations suggested that the association between Dellichthys and Evechinus might be close and that the former might recognise the urchin visually. Accordingly, brief studies were begun to investigate the nature of the association; the nature of the stimuli from Evechinus to which Dellichthys responded was experimentally investigated and gut contents of the clingfish were examined.

5.2b Methods

Clingfish were collected and kept with several Evechinus in running sea water laboratory tanks until the beginning of experiments.

To investigate the possible role of visual stimuli in attracting Dellichthys to Evechinus an oblong clear perspex tray equally divided into three was used (Fig. 6). The stimulus (e.g. an urchin)


stimulus
positive
2
1
0.5
0
0.5
1
2
negative
SCORE
5 cm

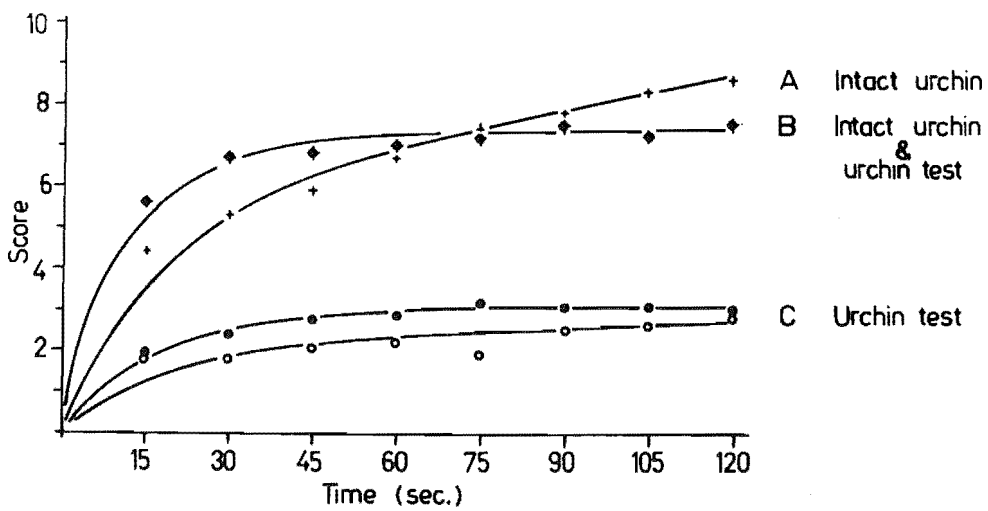

10
8
6
4
2
Score
15
30
45
60
75
90
105
120
Time (sec.)
A Intact urchin
B Intact urchin & urchin test
C Urchin test

Figure 6

Plan of apparatus used to test visual responses of Dellichthys morelandi. Positions of the fish were scored as shown.

Figure 7

Visual responses of Dellichthys morelandi in the apparatus of Figure 6. For explanation see text.

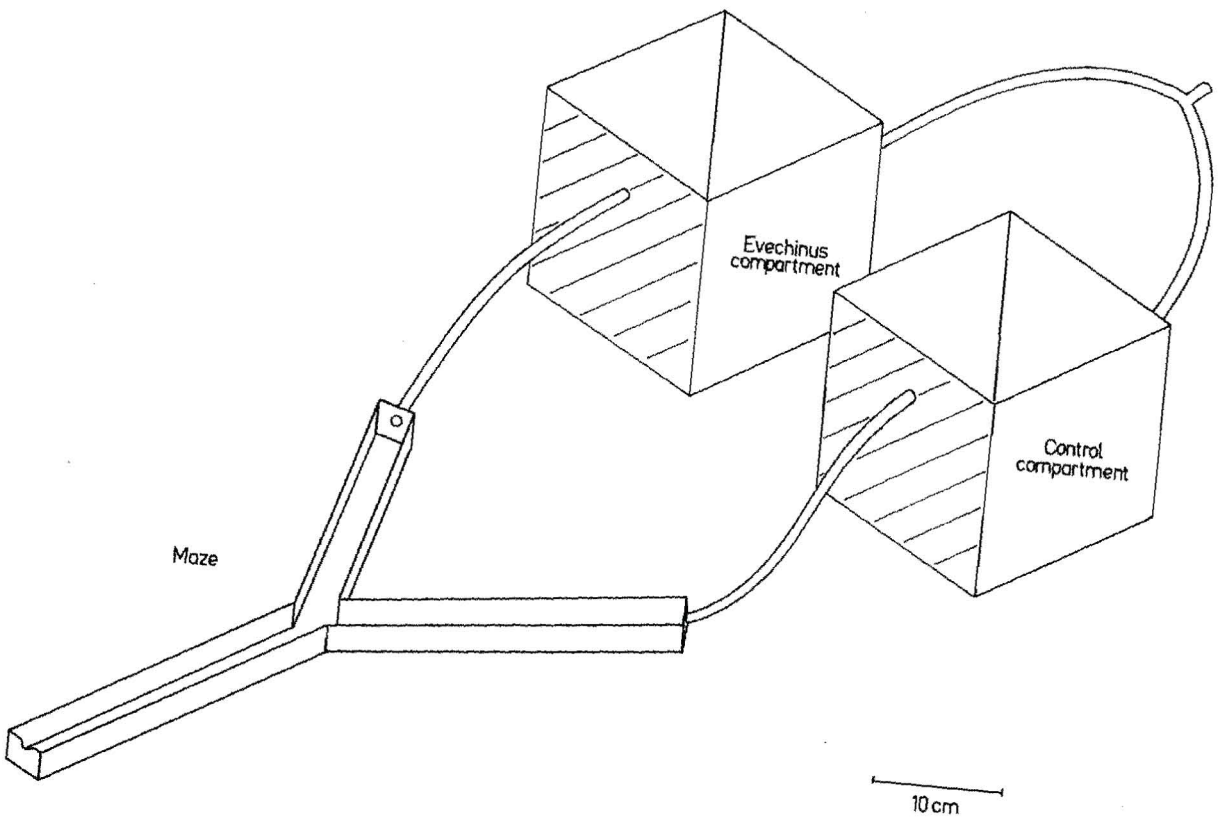

Evechinus
compartment
Control
compartment
Maze
10 cm

Figure 8

Apparatus used to test olfactory responses of *Dellichthys morelandi* to *Evechinus*.

was placed in one end section and five clingfish were introduced simultaneously into the centre of the central section. Positions of the clingfish were then noted and scored, as shown in Figure 6, at 15 second intervals for 2 minutes; scores were positive (maximum of 10) if the fish moved toward the stimulus, negative if away from it. Each run was repeated with the stimulus at the opposite end of the tray to minimise possible bias. Each double run was repeated five times using different clingfish and a mean score at each time interval was calculated for the ten runs. One set of runs was performed with an intact Evechinus as stimulus, two with similar sized Evechinus tests denuded of spines and one with an intact Evechinus in one end compartment and a denuded test in the other. In the last set, scores were positive toward the intact urchin and negative toward the test.

To see whether Dellichthys was chemically attracted to Evechinus a Y-maze perspex olfactometer through which unfiltered sea water flowed continuously from a constant head at about 400cc per minute was used (Fig. 8). Possible visual stimulation was eliminated by separating the Evechinus compartments from the maze and by shielding them from the fish; inlets and outlets in these compartments were arranged so that water flowed over the urchin before entering the maze. Five Dellichthys were placed at the tail of the maze and their positions were noted at five minute intervals for 30 minutes and again at 60 minutes. Positions were scored positive if the fish moved into the arm of the maze through which 'Evechinus water' flowed, negative if into the other. At the end of each run the apparatus was thoroughly washed in fresh water and for the next run the urchin was placed in the opposite compartment to minimise bias. New fish were used in each run.

Gut contents of two samples of 10 freshly collected Dellichthys were examined under dissecting and compound microscopes, one in May and one in July 1968.

5.2c Results

Visual stimuli

Mean scores for clingfish in the visual chamber are shown in

Figure 7. Although an overall attraction (positive score) is shown to a denuded test (Curves C) as well as to an intact Evechinus (Curve A) the intensity of attraction towards the latter is greater; some fish responded negatively towards the intact urchin but more did so towards a test. Further, the behaviour of the fish towards the two stimuli differed; fish which moved away from the test tended to remain immobile while those that initially responded negatively to the intact urchin did not settle down and tended to later move toward the urchin (in Figure 7, Curve A does not reach an asymptote but Curves C do).

That the clingfish are able to distinguish an intact urchin from a denuded test is indicated in Curve B where attraction toward the intact animal over-rules that toward the test. A few of the fish that moved toward the test end of the chamber tended to remain there producing the asymptote in Curve B.

Olfactory stimuli

Results of the choice chamber experiments are given in Table 9 where numbers and percentages responding (i.e. moving into the arms of the maze), type of response, ratio of positive to negative responses and tests of significance of the difference of the ratio from 1 are shown for each observation.

TABLE 9 : Responses in Choice Chamber from 30 runs with five Dellichthys morelandi per run*

TIME	RESPONSES					SIGNIFICANCE	
(min)	Number	%	+ve	-ve	+ve/-ve	χ^2	P
5	55	36.7	37	18	2.1	6.56	0.01
10	76	50.7	44	32	1.4	1.89	0.25 > P > 0.10
15	87	58.0	52	35	1.5	3.32	0.10 > P > 0.05
20	93	62.0	54	39	1.4	2.42	0.25 > P > 0.10
25	98	65.3	55	43	1.3	1.47	0.25 > P > 0.10
30	102	68.0	56	46	1.2	0.98	0.50 > P > 0.25
60	105	70.0	49	56	0.9	0.47	0.50 > P > 0.25

At the first observation (5 min) significantly greater numbers of fish responded positively than negatively although only 36.7% had responded by this time; more fish had responded positively than negatively at all observations up to 30 min but they tended to become evenly distributed in the maze (equal numbers in each of the arms and in the tail) at later observations.

Gut contents

Gut content analyses of 20 Dellichthys are shown in Table 10. All fish had material containing a purple pigment, apparently from the tube feet and/or pedicellariae in their hind gut and all except one had at least a part of a tube foot or pedicellaria in their gut. No food other than parts of Evechinus was found.

5.2d Discussion

The foregoing indicates a close association between Dellichthys and Evechinus. Independently, J. Moreland (pers. comm.), when collecting Dellichthys "always found them associated with Evechinus".

The stimuli from Evechinus to which the clingfish respond appear to be chiefly visual and although more experiments would be necessary for complete definition, the ability of the clingfish to distinguish an intact urchin from a denuded test suggests that the spines of Evechinus act as a sign stimulus; colour vision might also be involved since the denuded tests used in the experiments were a lighter colour than the intact animal. It is possible that the two fish, Aeoliscus strigatus and Diademichthys deversor, living among the spines of the long spined urchin, Diadema also respond to visual stimuli from the urchin (Davenport, 1966; Marshall, 1965).

The choice chamber experiments indicate that Dellichthys might also be chemically attracted to Evechinus but in the apparatus used the intensity of this response was not strong. It is possible that a process of habituation ("the ... waning of a response as a result of repeated stimulation in the absence of reinforcement" Thorpe, 1956; see also Clark, 1960) explains the fall in the ratio

TABLE 10 : Gut content analyses of 20 Dellichthys morelandi from Kaikoura

SPECIMEN	LENGTH (mm)	GUT CONTENTS				
		Tube feet	Xtalline plates*	Pedicellaria	C.S.R. pedicel*	Pigmented material*
1	24	10	-	-	-	++
2	22	8	2	-	-	++
3	21	7	-	-	1	++
4	20	3	4	-	-	++
5	17	2	-	-	-	+
6	20	6	-	-	-	+
7	17	-	-	1	2	+
8	17	1	-	-	-	+
9	15	-	-	1	1	+
10	14	-	1	1	-	+
11	29	-	-	1	-	++
12	26	-	3	-	-	+
13	25	1	-	6	1	++
14	25	-	1	-	-	+
15	23	1	-	-	-	+
16	22	1	-	-	-	+
17	22	-	-	2	-	+
18	20	3	-	-	-	++
19	19	-	-	-	-	+
20	18	-	-	1	-	+

* Note: Xtalline plates are from tube feet (one per foot)
C.S.R. Pedicel. = calcareous supporting rod of pedicellaria
Relative amount of pigmented material indicated by + or ++

of positive to negative responses since fish could not encounter an urchin in the maze.

Evechinus populations at Kaikoura are markedly clumped (Section 2.4a) and visual attraction could be important in maintaining the urchin-clingfish association, particularly if the clingfish move from urchin to urchin. Rapid and visually directed movement could ensure a minimum risk of predation while in the open. Laboratory observations have indicated that blennies (species not known) attack exposed Dellichthys but although these blennies have been observed among urchin populations, natural predation has not yet been observed. Visual attraction is also likely to be specific, ensuring that the clingfish reaches its source of food and shelter.

5.3 Summary

Syndesmis sp. (in the gut) and various ciliates (in the gut and gonad) were commonly found in Evechinus. Exosphaeroma sp., living beneath and among the spines of the urchin is possibly a close associate but Nauticaris marionis is probably not. Evechinus provides shelter and food for the clingfish Dellichthys morelandi Briggs. The latter appears to be attracted to the echinoid by visual recognition.

6. PREDATION

Moore (1966) stated that "despite the protection of their spines, urchins, even poisonous ones, have a number of enemies." These included mammals (sea otter and arctic fox), birds (eider duck, sea gulls and shore birds), various fish, echinoderms (asteroids and echinoids) and some molluscs. Other predators include crustaceans (Ebling et al., 1966 and Fielder, 1965) and an anemone (Dayton, Robilliard and Paine, 1968).

Predation upon healthy Evechinus was only directly observed once during this study. A blue cod, Parapercichthys colias, was seen to consume a juvenile urchin at St Kilda Rocks in January 1968. Numbers of Evechinus have been recorded from the gut of this species (G. A. Knox and various fishermen, pers. comm.) and also from the snapper, Chrysophrys auratus (J. Laxton, pers. comm.). Spear-fishermen consider that broken Evechinus are the best ground bait for the latter species.

Invertebrate predators include molluscs and sea stars. J. Laxton (pers. comm.) studied the cymatiid gastropods Charonia capax and C. rubicunda in the Leigh, Auckland area. While diving he observed individuals of both species crawling on to the test of Evechinus brushing aside the spines and then rasping a hole through the test. After immobilising the urchin with a salivary poison they began consuming them.

Other diving observations by Laxton (pers. comm.) showed that the sea star Cocinasterias calamaria was also a predator. The very similar Astrostole scabra is abundant at Kaikoura and it too probably attacks Evechinus since the urchin shows a marked escape response to it. This consists of a flattening of spines to enable pedicellariae to attach to the tube feet of the sea star as well as rapid movement from the latter; see also Jensen (1966). Astrostole with Evechinus tube feet attached were observed during diving and the seastar was also seen consuming tagged urchins although these may have been unfit or dead before attack.

Nothing is known of the predation pressure these animals exert on Evechinus.

In view of the wide variety of animals recorded as urchin predators (Moore, 1966; Randall, Shroeder and Stark, 1964), Evechinus probably has predators other than those listed. Further observations, particularly by diving, will be necessary to substantiate this opinion.

7. COVERING AND RESPONSE TO LIGHT

7.1 Introduction

Many echinoids cover, "decorate" or "mask" themselves with various substances; mainly pieces of algae, shells and pebbles. Harvey (1956), Hyman (1955) and Reese (1966) summarise the literature. Two major functions have been suggested: to conceal or camouflage the urchin or to protect it from light, and of these the latter has received most support (Lewis, 1958, Millot, 1956; and reviews by Millot, 1966, Nichols, 1964 and Yoshida, 1966).

Evechinus chloroticus covers itself in both intertidal and subtidal populations (Frontispiece, Plates 1 and 4). The following field observations, however, suggest that the habit may not be a simple light-avoidance response. Evechinus is often found covered in situations where light intensities are low (e.g. among small pebbles beneath fairly large rocks; in up to 30m of dirty water; in caves and underhanging crevices). In groups of urchins exposed to similar light intensities some may be covered, others may not be; further, only a small portion of an urchin may be covered (Frontispiece). Frequent observations on populations of Evechinus show that the extent of covering depends mainly on the availability of covering material. Thus after rough seas, when large amounts of algal debris drift about, more urchins become covered. This observation was also noted for Paracentrotus lividus by Gamble (1966). Further, dense aggregations of Evechinus often locally denude the substrate of algae. After calm seas when little drift algae is present, urchins in the centre of these clumps are often without cover while those around the edges, where algae is growing, are extensively covered.

To gain a general understanding of the covering process and to test the suggestion that covering is not simply a light avoidance response in Evechinus, investigations into the mechanisms and stimuli involved in the covering process were carried out and a series of experiments testing the following hypotheses was designed. If covering is a light avoidance response it would be expected that

Evechinus would (a) not cover when placed in dark or cover very little when placed in near-dark conditions, (b) show a physiological adaptation so that when placed in light animals which had been kept in darkness would cover more rapidly and more extensively than animals kept for the same period in light, and (c) cover less at night than during the day.

7.2 Material

Experiments were performed with subtidal (shallower than 10m) and intertidal Evechinus from Kaikoura, and subtidal (shallower than 3m) from Kaiteriteri. Prior to the experiments they were generally kept for several days in running seawater tanks. For the sake of continuity methods used in the various experiments will be discussed below.

7.3 Methods, results and discussion

7.3a Mechanisms and stimuli involved in the covering process

Two broad categories of covering material are utilised by Evechinus: material which is likely to drift on to the surface of an urchin (mainly algal debris), and material which is actively taken from the substrate (shells, pebbles). The mechanisms involved in moving materials over, and holding them against the urchin are similar to those described for Lytechinus variegatus by Millot (1956). Tube feet and spines move the material which is then held by tube feet.

In an investigation of the stimuli involved in the capture of floating material, Millot (1956) found that the tube feet of Lytechinus extended and attached to opaque cover slips floating above the illuminated aboral surface; they did not respond to clear cover slips. He concluded that tactile stimuli were "not significantly involved" but that a change in light intensity was important. When similar experiments were performed with Evechinus it was found that tube feet responded to neither opaque nor clear cover slips. But single, extended tube feet touched by a cover slip or other

solid material almost always attached. After several seconds other tube feet in the area of contact were extended to attach and then hold the material to the urchin. Touching the spines of Evechinus initiated a rapid response. Spines around the area of contact pointed towards the point of contact and after several seconds, if the material remained in touch, tube feet extended to attach and then hold the material to the urchin. The rapid spine response often held material against the urchin until the tube feet attached. Thus, in contrast to Lytechinus, tactile stimuli are most significant in the capture of floating material in Evechinus.

Further experiments showed that the tube feet of Evechinus are less responsive to changes in light intensity than those of Lytechinus variegatus (Millot, 1956) or of Tripneustes esculentus (Lewis, 1958). Resting Evechinus subjected to changes in light intensity either by shading natural or artificial light or by shining light on shaded specimens, showed no recognisable tube feet response. In contrast, Millot (1956) found definite responses to both increases and decreases in light intensity, the responses to shadows being the most striking. "In either case tube feet are quickly withdrawn and then, after a varying interval, slowly extended ..."

That tactile rather than photic stimuli are also involved in the capture and movement of material actively taken from the substrate by Evechinus is indicated by the observation that such materials are often captured for cover despite the fact that they do not cast any shadow on the urchin. This observation is reinforced by the results of an experiment in which an urchin was placed in a 25 x 22cm tray containing equal numbers of 25mm clear and black squares of 1.3mm perspex arranged in checkerboard fashion over the bottom. The number of squares of each type utilised as cover was noted at intervals from 0930 to 1630 hrs; throughout this period the urchin was generally lit by window light in the laboratory. This experiment was repeated 60 times using different urchins and the numbers of clear and black squares utilised as cover at 0.5, 2.5, 5.5 and 7.5 hrs after the start of experiments

are shown in Table 11. Observations were also made at 1.0, 1.5, 2.0, 6.0, 6.5 and 7.0 hrs but those shown are representative.

TABLE 11 : Number of clear and black squares utilised as cover by Evechinus

Time (hrs)	Number of squares		χ^2	P	Mean number per urchin	
	Clear	Black			Clear	Black
0.5	108	128	1.69	.25 > P > .10	1.8	2.1
2.5	120	160	5.71	.025 > P > .001	2.0	2.7
5.5	132	170	4.78	.05 > P > .025	2.2	2.8
7.5	116	160	7.09	.01 > P > .005	1.9	2.7

At 0.5 hrs the number of black squares utilised as cover did not differ significantly from the number of clear squares. Squares were thus utilised irrespective of colour suggesting that tactile stimuli were involved in the initial covering response. At subsequent intervals, however, after rearrangement and further uptake of squares, significantly greater numbers of black squares were utilised, suggesting that the urchin can distinguish between the two types. Although this might suggest that the urchins finally used the squares as shade the small numbers of squares used (Table 11) were insufficient to effectively shade the 6 - 8 cm urchins. Essentially similar experiments performed by Dubois (1914) with Strongylocentrotus lividus gave similar results. Dubois concluded that light evidently played a role in the orientation of objects but that it was not necessary to initiate the act of lifting.

In summary, it is concluded that the stimuli involved in the capture and initial uptake of both floating material and that taken from the bottom are tactile and not photic. As with Lytechinus (Millot, 1956) the tube feet of Evechinus show variable activity under conditions of uniform illumination or darkness, but Evechinus, particularly those in moving water, generally have at least a few tube feet extended and waving about. It is when these, or spines,

come into contact with covering material that the covering response is initiated. It is notable that Gamble (1966) suggested that covering in Paracentrotus lividus might not be an active shading response but "could be due to a local reflex on the part of the tube feet initiated by contact with any suitable surface."

7.3b Effects of light on covering

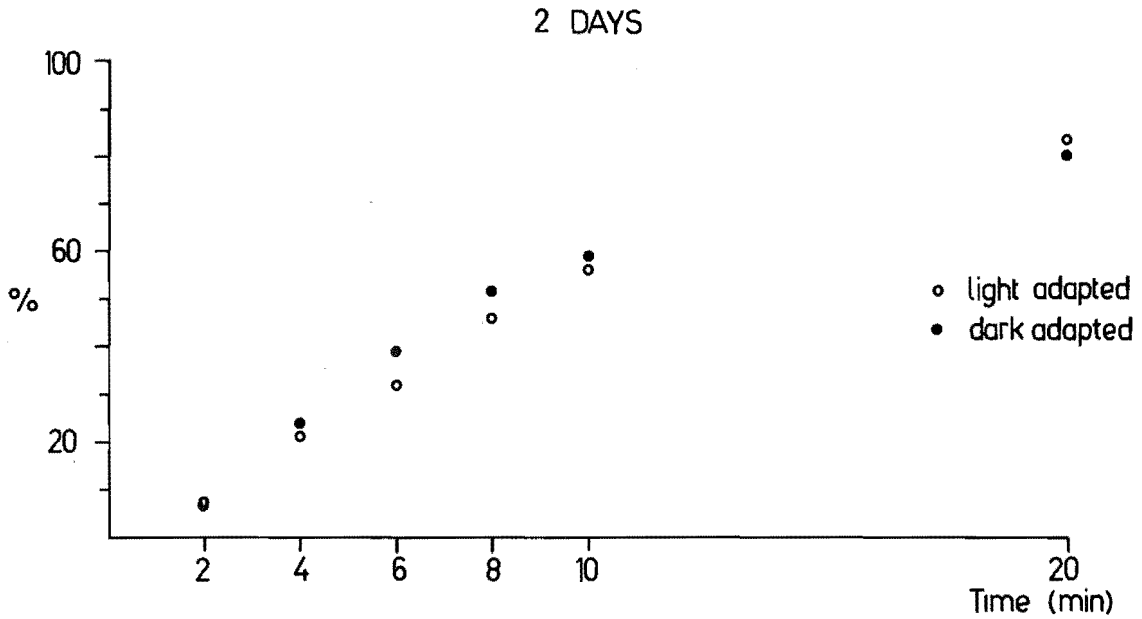
i. Covering under light and dark conditions

To test the effects of light intensity on the rate of covering and on the amount of cover adopted, five similar sized Evechinus collected intertidally at Kaikoura were placed in each of two 22 x 27cm trays, one being blacked out and the other being white and naturally lit (intensity of ca 6 on a Weston Master III light meter). For covering material 2.7cm discs of the brown alga Lessonia variegata were evenly spread in contiguous rows over the bottom of each tray. Immediately after placing in the trays the urchins began covering. The percentage of the surface covered was estimated at 2 min intervals to 10 min and then at 20 min by which time the urchins had settled down. Five such runs were performed using different urchins, all runs giving the trend shown in Figure 10 where mean percentages for all runs are plotted.

Since urchins in the blacked-out as well as the lighted tray covered at a similar rate and finally adopted similar amounts of cover (for the last observation $t = 0.76$ giving $0.5 > P > 0.4$) a tactile rather than light-avoidance response is suggested. Those in the lighted tray did, however, cover a little more rapidly suggesting that the response is affected by light.

ii. Does light and dark adaptation occur in the covering process and in the phototactic response?

Millot (1956) demonstrated a physiological adaptation in Lytechinus. When uncovered in strong light for a long period urchins ceased to show the covering response, but this reappeared after a sojourn in darkness. To test whether light and dark adaptation occurred in the covering process of Evechinus 10 urchins were kept in each of two running seawater trays, one blacked out


2 DAYS
100
60
20
%
2
4
6
8
10
20
Time (min)
light adapted
dark adapted

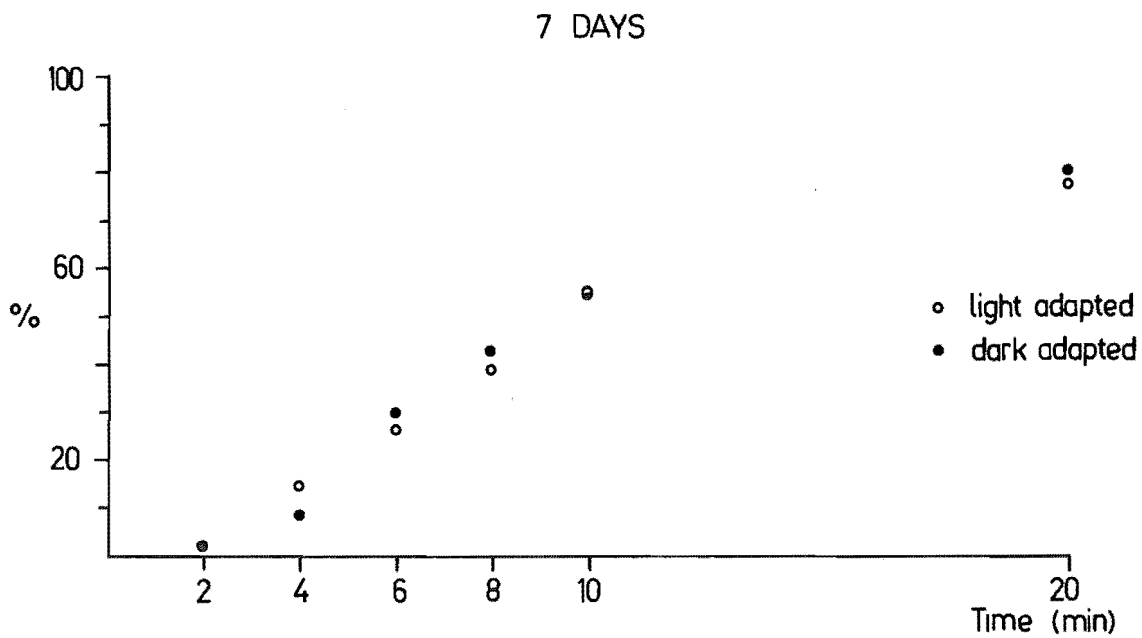
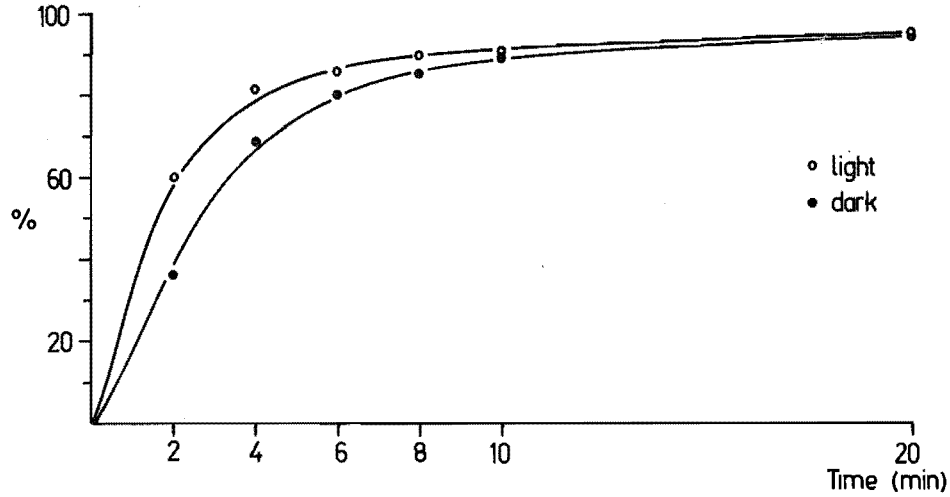

7 DAYS
100
60
20
%
2
4
6
8
10
20
Time (min)
light adapted
dark adapted

Figure 9

Rate of covering of dark- and light-adapted Evechinus. Urchins were adapted for 2 and 7 days. For further explanation see text.


100
60
%
20
2
4
6
8
10
20
Time (min)
light
dark

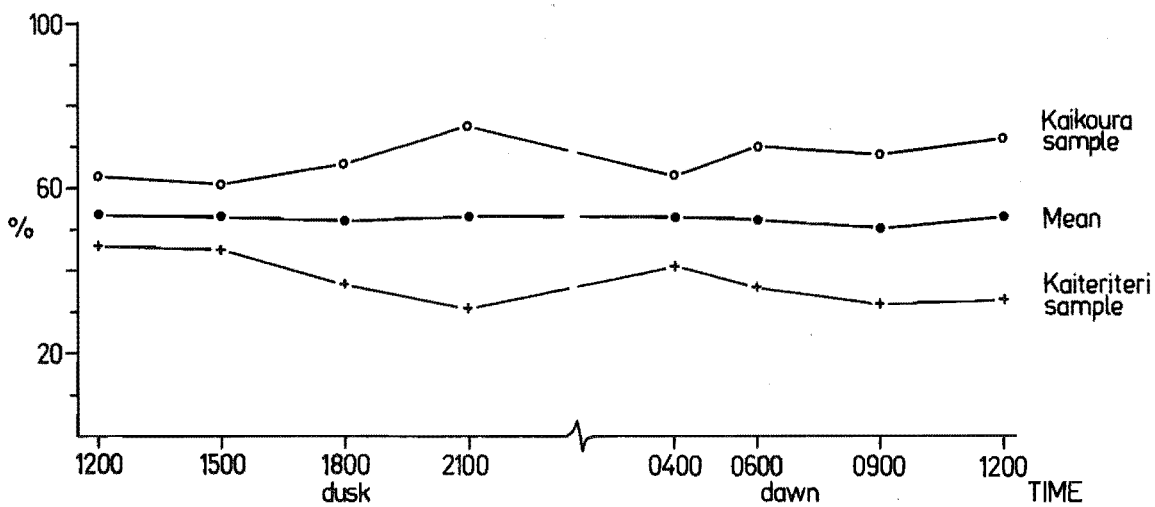

100
60
%
20
1200
1500
1800
dusk
2100
0400
0600
dawn
0900
1200
TIME
Kaikoura sample
Mean
Kaiteriteri sample

Figure 10

Rate of covering of Evechinus in light and dark conditions. For further explanation see text.

Figure 11

Mean percentages of test covered with algae over 24 hours in a naturally lit laboratory.

and the other lit by natural light supplemented by continuous light from an overhead 40watt tungsten filament lamp. Different groups of urchins were thus adapted for periods of two days and one week. At the end of the adaptation period the rate of covering of both light and dark adapted urchins was investigated in lighted trays as described for the previous experiment.

The mean covering rates of 70 light- and 70 dark-adapted urchins (adapted for two days) and those of 40 light- and 40 dark-adapted urchins (adapted for one week) are shown in Figure 9. There were no marked differences between the covering rates and amount of cover finally adopted of light- and dark-adapted urchins, either after adaptation periods of two days or one week. This suggests that physiological adaptation to light or dark does not occur in the covering process of Evechinus.

Light and dark adaptation can, however, occur in Evechinus as indicated from investigation of the phototactic response of animals as a whole. Half of a sample of ten urchins, light adapted for one week as above, were placed in the zero position of a 95cm x 15cm trough (Fig. 12). An equal number of dark adapted urchins was placed in an identical trough. The troughs were half covered with a black screen and had a clear end in the uncovered portion, this end facing a window and also being lit by a 40 watt tungsten filament lamp. Positions of the urchins were then scored as shown in Figure 12 at 15, 30, 60 and 90 mins. The experiments were then repeated with the other halves of the samples in the opposite troughs to minimise possible bias, and these runs were later repeated with different urchins. Under the scoring system used, photonegative responses were positive, increasing towards the darkened end of the troughs and photopositive responses were negative. Mean scores for 65 light- and 65 dark-adapted urchins (Table 12) indicate that the dark adapted urchins were more photonegative than the light adapted urchins, higher percentages moving away from the lighted end.

TABLE 12 : Phototactic response of light- and dark-adapted Evechinus. Higher scores indicate a more photonegative response.

	Mean scores		Percentage moving from the lighted end	
Time (min)	Light adapted	Dark adapted	Light adapted	Dark adapted
15	1.18	1.49	70.8	75.4
30	1.75	2.12	78.5	81.5
60	2.18	2.85	76.9	86.2
90	2.26	3.23	73.8	87.7

iii. Covering and diurnal changes in light intensity

Two samples of Evechinus (18 from intertidal Kaikoura and 20 from subtidal Kaiteriteri), maintained in running seawater tanks with abundant algae for food and cover for two weeks, were observed over a 24 hr period at the following times: 2 May 1968, 1200, 1500, 1800, 2100; 3 May, 0400, 0600, 0900, 1200. During this time the tanks were naturally illuminated. At each observation the percentage of the surface of each urchin covered by algae was noted; mean percentages for each sample and means for both samples combined are shown in Figure 11.

The urchins did not show any tendency to drop cover during darkness and assume it again in light. This behaviour contrasted with that observed in a natural population of Lytechinus variegatus by Millot (1956) and in aquarium-kept specimens of this species (Sharp and Gray, 1962), where the extent of covering was related to diurnal light changes.

7.4 General discussion

In contrast with the covering behaviour of Lytechinus variegatus and Tripneustes ventricosus (Millot, 1956 and Lewis, 1958) that of Evechinus seems very little directly related to light or

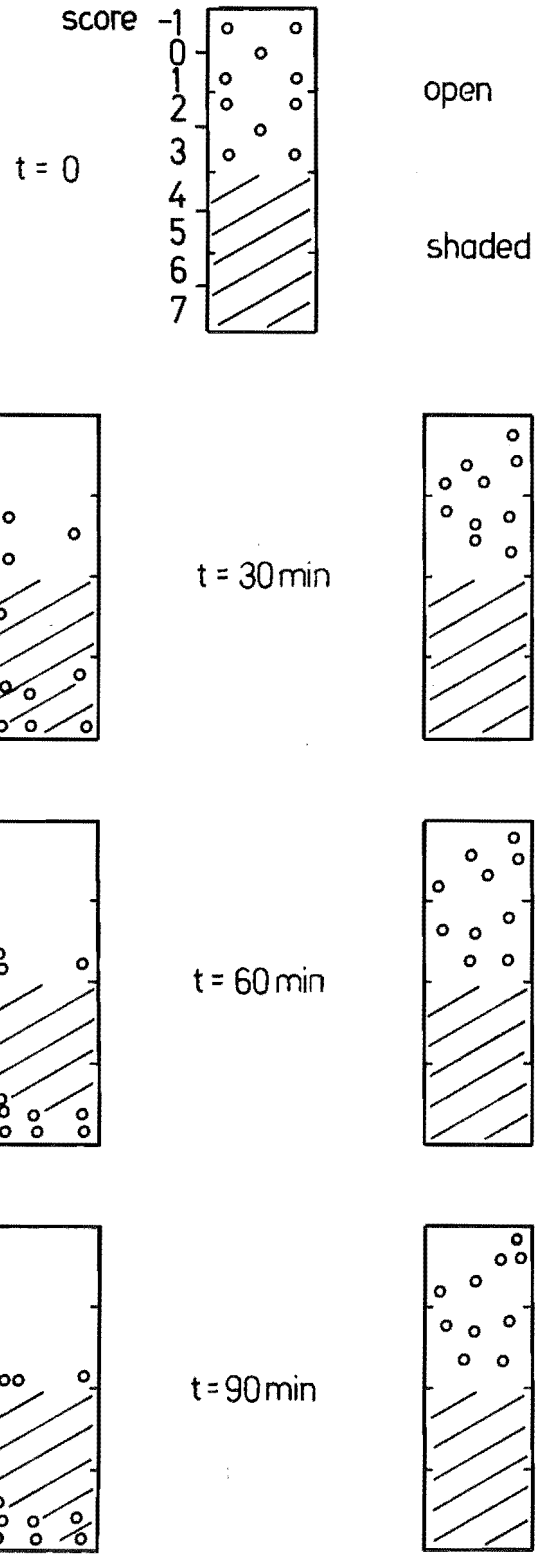

score
-1
0
1
2
3
4
5
6
7
t = 0
open
shaded
t = 30 min
t = 60 min
t = 90 min
cover
no cover
cover
no cover
RUN 1
RUN 2

Figure 12

Movements of Evechinus (indicated by circles) with and without cover. Positions of urchins were scored as shown at the top of the figure. Thus, the mean score of Run 1, no cover, 30min is 0.1 (2x2 + 3 + 4 + 3x6 + 3x7), i.e. 5.0.

to light avoidance. The stimuli involved in the capture and initial uptake of covering material are tactile and not photic. Cover is taken up in both light and dark and although the rate is slightly faster in the former, the final amount of cover adopted does not differ between the two. The covering process (both rate and final amount of cover) is not affected by adapting the urchin to light and dark conditions and the extent of covering does not show diurnal changes. Field observations cited in the introduction reinforce this conclusion.

It appears that the covering reaction in Evechinus is related to the positive reaction of the podia to contact; not an active shading response (see also Gamble, 1966 and Reese, 1966). What adaptive functions could this tactile response serve?

That the habit may indirectly function in light avoidance is shown by the movements of 10 Evechinus placed in each of two half shaded and half lit troughs (Fig. 12), those in one trough having abundant mixed algal cover and those in the other being without cover. Movement of those without cover into the shaded part of the trough was much more than those with cover (Fig. 12).

This function may be more important in intertidal than in subtidal populations. Intertidal urchins, if not concealed, are likely to be subjected to stronger light intensities than subtidal urchins. Field observations suggested that intertidal urchins typically had more cover (often of shells or stones: Section 2.1) or were more concealed than subtidal urchins; they also appeared to cover faster and more extensively in laboratory experiments.

As suggested for other species of urchin (references, Section 7.1) the tactile covering response in Evechinus could serve to camouflage small individuals which may be eaten by some fish (Section 6). However, it is doubtful that covering serves this purpose in large Evechinus since these are generally covered far less than small specimens and are often found in the open without cover (Frontispiece, Plate 4). Further, known and possible predators of large Evechinus are invertebrates (Section 6) which could not rely on image perception for capture of prey.

Diving and other field observations suggest that the covering response in Evechinus may be mainly related to the capture of food:

(a) The covering material of 100 Evechinus at Kaiteriteri and 80 at Kaikoura examined during diving observations on feeding in February 1968 is shown in Table 13.

TABLE 13 : Materials used as cover by Evechinus at Kaikoura and Kaiteriteri*

Kaikoura		Kaiteriteri	
Covering material	Percentage	Covering material	Percentage
Brown algae	30.0	Carpophyllum	9.0
Red algae	16.4	Shell	6.0
Red + brown algae	22.4	Leaf	4.0
None	31.2	Stick	4.0
		Carpophyllum + Hormosira	3.0
		Carpophyllum + shell	1.0
		Carpophyllum + leaf	1.0
		Shell + stone	1.0
		Shell + leaf	1.0
		Leaf + stone	1.0
		Stick + leaf	1.0
		Stone	1.0
		None	67.0

* Based on samples of 80 at Kaikoura and 100 at Kaiteriteri in February 1968.

All substances utilised as cover were found to be also utilised as food (see Section 4.3), and at Kaiteriteri, where a wider variety of cover was found, Carpophyllum and shell, the two most frequent covering materials were also the most frequent sources of macroscopic food. At Kaikoura, where cover consisted entirely of algae, food consisted mainly of similar algae.

(b) Both in nature and in aquaria, Evechinus was often found with a piece of alga wrapped around the test, this being cover on top and food underneath.

(c) During January 1969, Evechinus were collected every three days from a population occupying a localised barren area (see Section 10.3a). Over most of this period seas were calm, Evechinus were little covered, few were observed feeding and the gut of animals examined contained little algal food but considerable amounts of bottom material. Towards the end of the sampling period rough seas produced large amounts of drift algae. The urchins became extensively covered and all were observed to be actively feeding in the field.

Drifting algal debris must form a significant food source for Evechinus, particularly for populations living in localised barren areas. P. K. Dayton (pers. comm.) independently suggested that the covering response in Strongylocentrotus purpuratus is maintained as a feeding device for this animal often derives most of its food from drift algae. Ebert (1968) also suggested that the algae held on the spines and tube feet of S. purpuratus was utilised for food. Otter (1932) suggested for urchins in general that "algae and other food may be carried by wave action on to the tube feet around the anal pole ... and handed by them to the mouth below."

A further and interesting function is served by covering in the Antarctic urchin Sterechinus neumayeri (Dayton, Robilliard and Paine, 1968). This urchin is preyed upon by the actinarian Urticinopsis antarctica. Twenty in situ experiments showed that when an urchin covered with a mat of hydroids comes into contact with an anemone "the anemone places its tentacles over the potential prey, touches the hydroids and then often retracts its tentacles, thereby releasing the urchin." Release occurred in 80% of the experiments but uncovered urchins induced to crawl against the same anemones were always captured and consumed.

7.5 Summary

1. Field observations suggested that the covering

response in Evechinus was not a simple light avoidance response but was related to the positive reaction of the podia to contact. The following laboratory observations supported this suggestion:-

(a) the stimuli involved in the capture and initial uptake of covering material were tactile and not photic; (b) cover was taken up at a similar rate in both light and dark conditions; (c) the covering response did not show adaptation to light or to dark, in contrast to the phototactic response, and (d) the extent of covering did not show marked diurnal changes.

2. While the covering response may indirectly serve in light avoidance in some situations, more likely functions are camouflage in small urchins and capture of food (particularly algal debris) in both small and large urchins.

8. GENERAL DISCUSSION AND CONCLUSIONS

Features of the general biology of Evechinus differ between geographical areas. This is particularly evident in the Kaikoura and Kaiteriteri populations.

Summarising, these populations differ in at least: (a) vertical distribution, both intertidal and subtidal; (b) morphology, spination and relative test thickness; (c) feeding habits, proportions of browsers and algivores, and (d) covering, types of covering material.

Some of these differences appear to be environmentally induced. Differences in spination are probably related to amounts of wave action while test thickness is at least partly related to the amount of food available. The feeding habits reflect the food available, browsers being dominant where macroscopic algae are sparse and algivores where these algae are abundant. The types of material utilised for cover are similarly related to the types available in the environment.

Other biological differences (e.g. vertical distribution) probably also relate to environmental differences although further study is needed to clarify relationships. The possibility of genetic differences between populations is briefly discussed in Section 13.

9. DISPERSAL

9.1 Introduction

Because of two distinct phases in the life of Evechinus (a free-swimming larval phase and a benthic post-metamorphic phase) dispersal or movement occurs in two distinct ways. Larval dispersal and adult movement are therefore considered separately in this section.

The extent of larval dispersal depends mainly on the length of free-swimming larval life and the current systems in which the larvae live. Very few details are known of the coastal current systems in New Zealand (J. Brodie, pers. comm.) and investigation of these was beyond the bounds of this study. Rearing experiments were, however, used to estimate the length of larval life.

9.2 Larval life span and larval dispersal

9.2a Introduction

Evechinus chloroticus develops indirectly (Mortensen, 1921). Although Mortensen was unable to rear Evechinus to metamorphosis his two larval cultures lasted at least 35 days; the 8-armed plutei produced indicated that the larvae "take a comparatively long time to develop". Maxwell (1957) carried out further studies on development and survival of E. chloroticus larvae under various conditions of temperature and salinity but although his larvae survived from 6 to 17 weeks they did not feed and none developed further than the four armed pluteus stage.

The rearing experiments noted here were made to obtain a further estimate of the length of larval or dispersal life. They are an adjunct to studies on the composition and distribution of Evechinus populations.

9.2b Methods

Eggs and sperm were obtained from dissected gonads at Kaikoura; sperm being diluted before adding to eggs in culture dishes. After one to two days embryos were transferred to jars containing 1500cc

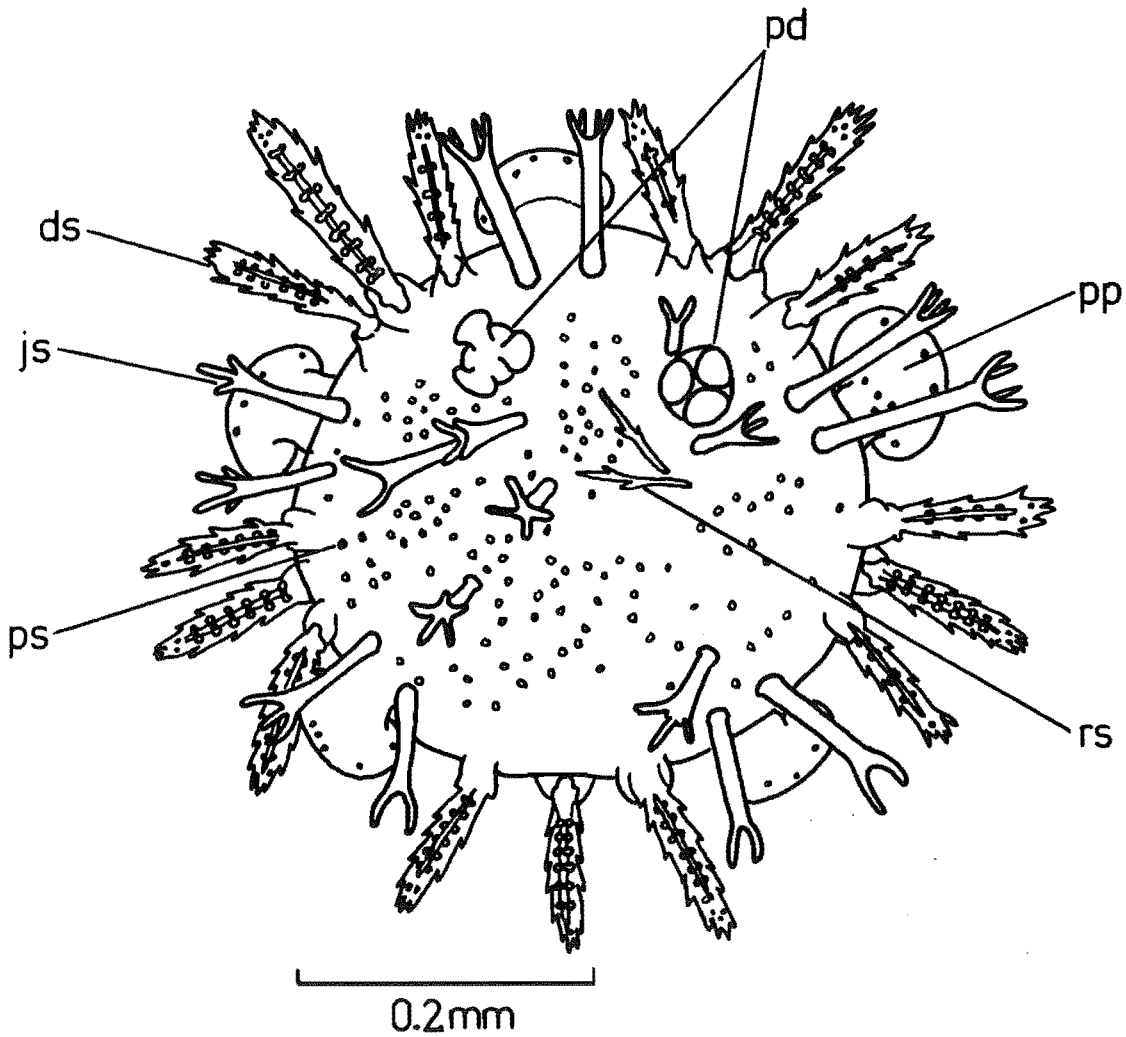

pd
ds
pp
js
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Figure 13

Aboral view of newly metamorphosed Evechinus chloroticus. Abbreviations: ds, definitive spine; js, juvenile spine; pd, pedicellariae; ps, pigment spot; pp, primary podium; rs, remains of larval skeleton.

of unfiltered sea water; these had previously been submerged for one week in running sea water to allow algal growth to form on the glass and provide food.

The cultures, at approximately 19°C, were aerated infrequently; no extra food was provided to the first three (Table 14) cultures but the diatom Phaeodactylum tricornutum was added to the fourth. Cultures 1 and 4 did not have a water change but culture 2 had a part water change after 29 days. Culture 3 had a complete water change after 29 days and became extinct the next day.

Cultures were usually examined daily to note the developmental stage of larvae, these stages being referred to the figures of Mortensen (1921, Plate X); the figures shown were designated as Stage I, II and III plutei. A further stage was recognised: fully formed plutei, otherwise similar to Stage III plutei, showed either one or two juvenile pedicellariae posteriorly. As soon as fully formed plutei were present the sides of the culture jars were examined for newly metamorphosed animals.

9.2c Results

Of the four cultures attempted, one gave fully formed larvae but three gave metamorphosed Evechinus.

Times, in days after fertilisation, at which different larval stages were first noticed are shown in Table 14 where data extracted from Mortensen (1921) are included for comparison. Since Maxwell's cultures did not develop beyond the Stage I pluteus his data are not included. Although larval densities were not high in the present study, considerable mortality occurred during development and metamorphosis, only six newly metamorphosed Evechinus (Fig. 13) being obtained.

9.2d Discussion

While developmental times were shorter than those recorded by Mortensen (1921) the larval life span of E. chloroticus under the above laboratory conditions is fairly long (about one month).

TABLE 14 : Developmental times, in days after fertilisation, for Evechinus cultures.

Culture*	Fertilisation	Stage I plutei	Stage II plutei	Stage III plutei	Fully formed plutei	Newly Metamorphosed Evechinus
1	Oct.67	5	15	17	+	36
2	Nov.67	4	13	15	22	30
3	Dec.67	5	10	13	17	-
4	Jan.68	4	11	14	21	28
Mortensen	-	6	21	35	-	-

* for conditions see text

\+ culture not observed

Although it is difficult to extrapolate laboratory data to field situations, Thorson (1961) was of the opinion that most laboratory rearings carried out at several degrees Centigrade higher than local sea temperatures (as was the case in the present study) would give an estimate of larval life which "will hardly deviate much from the average figures in Nature". Thus an average natural larval life span of about one month is indicated for E. chloroticus although it is likely that considerable variation occurs; larvae might settle sooner if provided with more favourable conditions since in the present rearings fully formed larvae were present about three weeks after fertilisation; on the other hand, Maxwell's 1957 study indicates that larval life may be extended to at least 17 weeks.

The relatively long free-swimming larval life indicates that larval dispersal may often be considerable. This is possibly reflected in the geographical distribution of Evechinus for it ranges not only the whole of the New Zealand mainland and nearby islands but also the Snares and the Chatham Islands (Section 1.3).

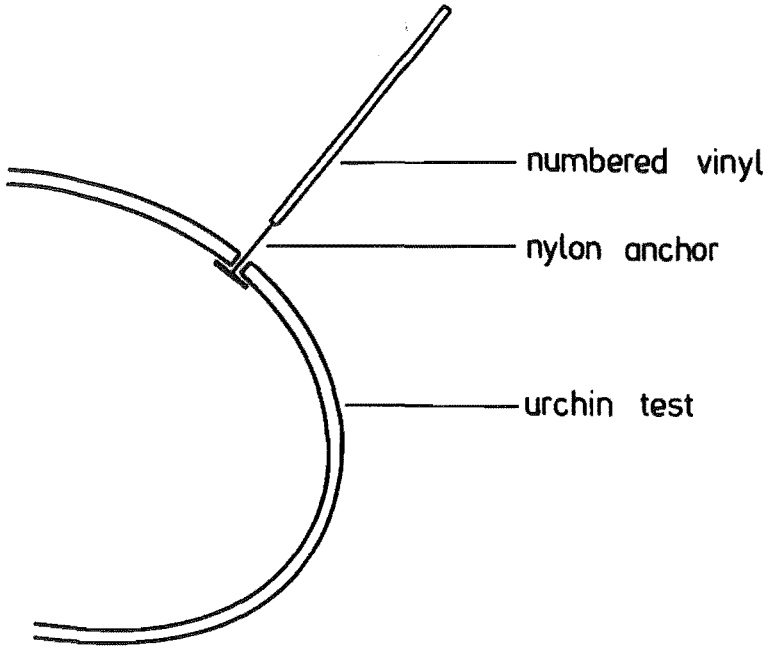
9.3 Tagging and adult movements

9.3a Introduction

Several workers have, with varying success, tagged sea urchins. These studies were aimed at investigating growth (Ebert, 1965a and b, 1967a, 1968; Fuji, 1962, 1963; McPherson, 1965, 1968), long-term movement (Fuji, 1963; McPherson, 1965, 1968) and short-term movement (Gamble, 1966; Neill and Larkum, 1966; Sinclair, 1959).

The present study aimed to investigate long-term movement in adult Evechinus at Kaikoura and also Kaiteriteri. Because of favourable results in preliminary experiments anchor tags were used; their effects on Evechinus were tested by comparing tagged and untagged urchins.

Studies of long-term movement aimed at testing the hypothesis, suggested by field observations, that Evechinus moved very little at Kaikoura but moved more at Kaiteriteri.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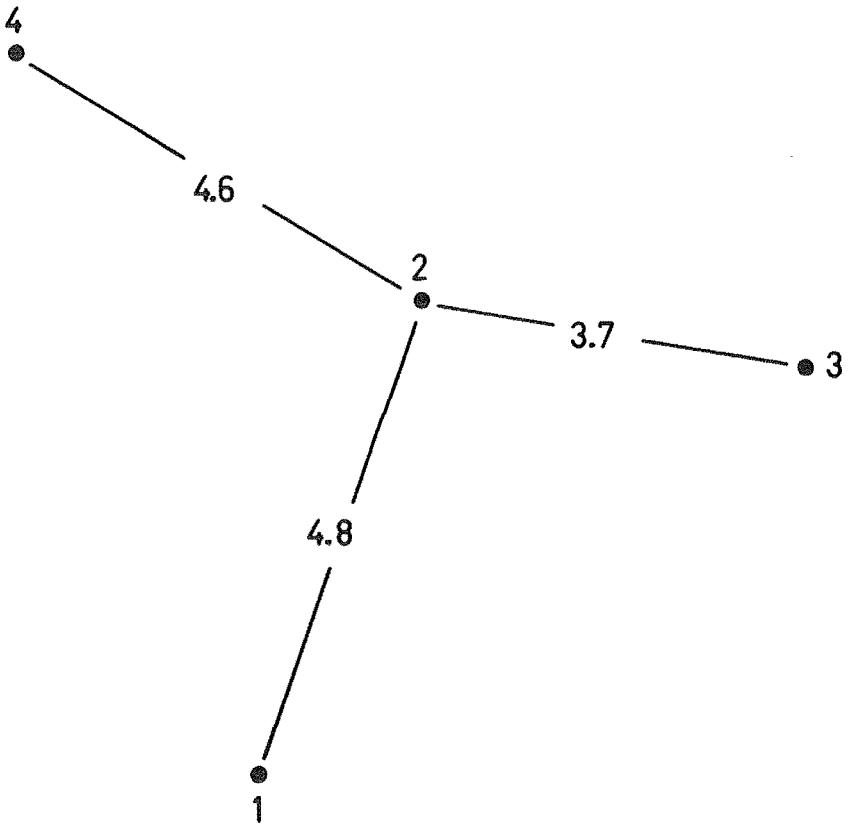

4
4.6
2
3.7
3
4.8
1

Figure 14

Diagram of anchor tag in place in the test of Evechinus.

Figure 15

Distances in meters between tagging sites in Third Bay, Kaikoura.

9.3b Materials and methods

Numbered vinyl spagetti tags with a nylon T-bar for anchorage (Fig. 14; see also K. N. Thorson, 1967) were used. These tags, originally designed for fish by Floy Tag and Manufacturing Ltd (catalogue number FD-67) were inserted through an interambulacrum towards the top half of the aboral surface (Fig. 14) using the tagging gun supplied by the manufacturers. It was unnecessary to drill a hole for insertion since the needle of the tagging gun could be pushed through the test.

Since these tags had not previously been used on urchins, preliminary trials were carried out. Five urchins were tagged and placed with untagged controls in a running seawater tank. They were maintained from July to December 1967, externally examined each month and in December were internally examined. In a second trial, 15 anchor-tagged were placed with controls in a low water pool on 30 October 1967. At the same time, 15 were also tagged using Ebert's (1965a), (= Fuji's 1962) nylon loop method. The urchins were collected and examined one month later. In a third trial, 15 subtidal urchins from a marked rock in 6m of water were tagged and replaced on 9 November 1967; they were externally examined on 16 December 1967 and on 8 January 1968.

The major tagging programme was carried out in December 1967 and January 1968 on a subtidal population of Evechinus in a depth of about 6m at Third Bay, Kaikoura. The positions of four neighbouring aggregations of urchins were marked using 1m lengths of yellow hose anchored to large rocks by 13cm galvanised steel bridge spikes which were hammered into the rock. The spacing of these markers was later measured and is shown in Figure 15. During tagging all urchins within 1m of each marker were removed and placed in a large wire basket. They were then brought to the surface, measured and tagged. After each urchin was tagged it was returned to the basket suspended in the water at the side of the dinghy to minimise time out of water. After a group of urchins was tagged the basket was lowered and the urchins were returned to the rock they had been taken from. In this way 90, 88, 46 and 86 urchins

were tagged at markers 1, 2, 3 and 4 giving a total of 310 tagged urchins.

The aggregations at the markers were systematically examined by diving after approximately three, six and nine months in March, June and September 1968. Although most effort was expended in searching for tagged urchins near the marked sites an extensive search of the general area was made in September, and similar but less intensive searches were made within the three-monthly intervals. In March and June the numbers of the tagged urchins were noted in situ and the number of untagged urchins at and around the markers was estimated. In September all the tagged urchins which could be found and a sample of untagged urchins were collected; test size, gonad condition, amount of food in the gut and condition of the test around the tag were noted.

A recovery history of individual animals was constructed to see whether animals which were noted on the second and third recaptures had been overlooked on the first and second.

On 7 October 1968, 27 Evechinus (5 to 6cm diameter) were tagged in situ on a large subtidal rock at Kaiteriteri. The tagging site and surrounds were examined in clear water one month later.

Movements of Evechinus were investigated in two running sea water trays in a naturally lit laboratory over a 24hr period. Each tray, 1m square and 12cm deep, was equally divided by a double netting partition; animals on one side having, and having had, abundant algal food with those on the other side having, and having had, no macroscopic food. Forty animals from Kaiteriteri (20 with and 20 without food) and 36 animals from Kaikoura (18 with and 18 without food) were observed at the following times: 2 May 1968, 1200, 1500, 1800, 2100 hrs; 3 May, 0400, 0600, 0900 and 1200 hrs.

Positions of all urchins were plotted on a scaled grid at each observation. Although animals were not tagged, it was assumed that if their arrangement did not alter between observations no movement had occurred. There was no reason to suspect rearrangements and/or homing movements which would not alter spatial distributions between observations. However, considering this possibility and also that

distances moved were calculated on the basis of straight line movement, distances summarised in Table 17 are necessarily minimum estimates.

9.3c Results

i. Tagging trials

Of the five urchins tagged in July 1967 and maintained in the laboratory all were alive and showed no spine loss after six months, although the smallest specimen (7.0cm diameter) was found to have no food in its gut and to have small shrunken gonads; the tag insertion hole in this specimen was enlarged and was internally surrounded by a dark soft pigmented material. The other tagged specimens had abundant food in the gut and ripe gonads. The tag hole in these specimens was not enlarged but was not sealed by test; a small ring of pigmented material surrounded it. All untagged specimens had ripe gonads and abundant food in the gut. No significant change in test diameter occurred in any of the urchins.

Thirteen of the 15 anchor-tagged urchins placed in the low level pool were found alive after one month, and one was found dead. Of these specimens six showed no external signs of tag effects, three showed a small amount of spine loss around the tag and four showed general spine breakage over the whole surface. The 15 untagged urchins were recovered, seven in healthy condition, but eight showing general spine breakage. Only eight urchins tagged with nylon loops were found alive; one was subsequently found washed-up.

Thirteen of the 15 urchins tagged and placed on the subtidal rock were found on the same rock one month later; none showed external signs of tag effects. Two months after tagging 14 were found on the same rock, 12 being apparently healthy and two showing slight spine loss around the tag insertion hole.

ii. Tag recoveries

The total number of tagged urchins noted from the four markers at each recovery is shown in Table 15.

TABLE 15 : Tagged Evechinus noted at each recovery in Third Bay

	Recovery		
	1 March	2 June	3 September
Number	178	80	53
Percentage of 310*	57.4	25.8	17.1

* tagged in December 1967 and January 1968

Some urchins were not noted on each recovery dive. Of the 80 tags noted on the second recapture 17 had not been noted on the first and on the third recapture 6 had been noted on the first but not the second and three had not been noted on either the first or the second. Further, from a sample of 37 apparently untagged animals collected at the markers on the third recapture, six were subsequently found to have lost tags. Thus the number of tagged urchins present in the population was higher than that indicated in Table 15.

Ten, five and ten tagged urchin shells were found near the markers during the tag recoveries and in September two tags were found lying on the sea bottom.

On 6 November 1968, one month after tagging, four (15%) Evechinus were found alive and apparently healthy at Kaiteriteri; two were found dead and tags were found from two; another had been washed up on 26 October.

iii. Distribution of recoveries

The distribution of recoveries for the first and second recaptures is shown in Table 16.

In March only 6% and in June only 9.9% of the noted tagged animals were recovered at markers other than those at which they were tagged. All of these came from the nearest neighbouring

markers. No tagged animals were found on rocks other than those at the markers.

TABLE 16 : Distribution of tagged Evechinus at marked sites in March and June 1968

Where marked	Where and number recovered							
	March				June			
	1	2	3	4	1	2	3	4
1	45	2			28	1		
2		44	4	1		21	4	1
3		7	20			2	8	
4		2		53				15

Of the live tagged urchins recovered at Kaiteriteri one was found at the tagging site and one was found at each of three positions, 3m, 4m, and 5m from the tagging site.

iv. Comparison of tagged and untagged urchins in September.

The most noticeable internal difference between tagged and untagged specimens was in the gonads. Only five of the 50 tagged specimens had gonads of normal size and appearance. Most had small, dark brown, tough-textured gonads which contrasted with the large, orange-yellow, soft-textured gonads of untagged animals. The size difference is clearly shown by the mean gonad indices; for tagged animals, 0.43 ($s = 0.29$); for untagged animals, 1.12 ($s = 0.24$). This is a highly significant difference ($t = 10.89$ for 78 d.f. has $P < 0.001$). All of the untagged but only eighteen of the tagged urchins could be sexed and gonads of tagged urchins contained many more red puncta (Kawamura, 1965) and also many more protozoa (mainly ciliates).

Although all tagged specimens had food in their gut, the quantity (subjectively estimated) was often less than that of

untagged specimens.

The tag insertion hole was never sealed by regenerated test (c.f. Ebert, 1965a) although a wad of darkly pigmented soft material had invariably formed in the inside of the test around the tag anchor and hole. In some specimens the tag insertion hole was enlarged and in 23 cases spine loss had occurred around the tag; 8 of these had lost spines over an area of about $1cm^2$, the rest over a smaller area. Eight showing conspicuous spine loss were also noted in March and four in June; none of these specimens was subsequently recaptured.

v. Diameter at tagging and recapture

The mean diameter of 51 tagged specimens recaptured in September 1968 (10.55; s = 1.05cm) did not differ significantly from that at tagging in December 1967 and January 1968 ($t = 4.8 \times 10^{-2}$ for 100 d.f. has $P > 0.9$).

vi. Laboratory movements

Movements of Evechinus in running seawater trays (Table 17) clearly show that the extent of movement may be related to the amount of food available; those specimens with abundant food moved less than those without. Results also indicate that more movement occurred during the night. Kaikoura specimens also moved less than those from Kaiteriteri.

9.3d Discussion

The anchor tags did not appear to seriously harm Evechinus during the preliminary trials, although one laboratory-kept specimen apparently ceased feeding and some of those in the pool and Third Bay lost a few spines around the tag. The tagging method was much more rapid than that of Fuji (1962) and Ebert (1965). This was important since the author had to collect the urchins by diving, measure and tag them and then return them to their collection site with assistance only from a person keeping records.

The recovery rate at Third Bay three months after tagging was high (more than 57%) but showed a marked decline after this.

TABLE 17 : Movements of Evechinus in running seawater trays

KAITERITERI SPECIMENS	FED (20)	STARVED (20)
Time	Minimum movement since last observation	
1200	-	-
1500	2 moved up to 3cm	1 moved 35cm
1800 (dusk)	No movement	2 moved, 12cm and 25cm
2100	1 moved 7cm	10 moved, some probably 38cm
0400	3 moved up to 7cm	12 moved, some probably 38cm
0600 (pre-dawn)	1 moved 7cm	8 moved, some probably 38cm
0900	No movement	2 moved, 12cm and 38cm
1200	No movement	1 moved 38cm

KAIKOURA SPECIMENS	FED (18)	STARVED (18)
1200	-	-
1500	1 moved 7cm	1 moved 7cm
1800 (dusk)	1 moved 7cm.	1 moved 7cm
2100	3 moved, up to 12cm	4 moved, up to 12cm
0400	4 moved, up to 12cm	7 moved; 2, 64cm, 5 up to 12cm
0600 (pre-dawn)	2 moved, up to 12cm	6 moved, up to 7cm
0900	1 moved 7cm	4 moved, up to 7cm
1200	No movement	1 moved 7cm

Only 15% were recovered alive one month after tagging at Kaiteriteri. Three factors have to be considered in seeking an explanation for fall in recoveries: movement, mortality and tag loss.

Movement did not appear to be significant at Kaikoura (Section 9.3c iii). Although anchor tags harm Evechinus, the recorded small amount of long term movement is considered typical for the urchin at Kaikoura since (a) the urchins generally form depressions or bare spots on the rocks where they are found (Section 2.1); (b) urchin-made depressions were not recolonised by other urchins for at least several months after the original inhabitants were removed at Seal Reef; (c) samples of 35 urchins were collected every three days for over a month from a dense aggregation occupying ca 12m^2 at Sharks Tooth Point (Section 10.3a ii). The bare areas left by the removal of these samples were not reoccupied by the end of the sampling programme despite the fact that over 100 urchins remained; (d) no conspicuous changes in the number of urchins at marked sites or on other conspicuous rocks in Third Bay was recorded between December 1967 and September 1968.

But Kaiteriteri recoveries, although few, indicated that more movement occurred in that area. This conclusion is also substantiated by other observations: (a) self-made depressions or bare spots were not evident beneath Kaiteriteri Evechinus. Although urchins were sometimes found in depressions these were not clean in contrast with those at Kaikoura; (b) 208 urchins were collected from a 30 x 2m strip in September 1967 and 190 were collected along the same strip two months later; and (c) urchins were on several occasions observed moving over subtidal rocks at Kaiteriteri but, despite more observation, this was never observed at Kaikoura.

Ebert (1967a) discussing the fall in recoveries of tagged Strongylocentrotus purpuratus considered that movement was not significant while Fuji (1963) did not recover tagged Hemicentrotus pulcherrimus "other than where they were released." McPherson (1965 and pers. comm.) stated that "Tripneustes ventricosus showed little movement", but he found tagged urchins up to 30m from the tagging sites. Leighton, Jones and North (1966) found considerable

movement in populations of S. purpuratus, S. franciscanus and Lytechinus anamesus living in areas locally denuded of algae but found that when these urchins received abundant food in the form of drift algae they "ceased foraging altogether." Kitching and Ebling (1961) also found that Paracentrotus lividus "is fairly active except in the presence of food." Thus, different urchins appear to move different amounts and, in a particular species, the extent of movement depends on the environmental conditions in which they are living. It seems probable that Kaikoura urchins move less than those at Kaiteriteri because they receive greater amounts of food, both of growing and drifting algae. That the extent of movement is related to availability of food is suggested from the laboratory observations on movements of Evechinus with and without food; those without food moved much more than those with.

Mortality is considered to be the most important factor in bringing about reduced recoveries since several dead tagged urchins were found every time the tagging sites were inspected at Kaikoura, and since three dead tagged urchins and two tags were recovered at Kaiteriteri. Urchin tests are light and fragile and since Third Bay is frequently exposed to strong wave surge which would break or remove the tests, more mortalities than those observed probably occurred. Apart from the three-monthly recovery observations the area was inspected at only three other times between tagging and final recovery. Further, those urchins with bare spots around the tag in March and June were not recaptured again; these had probably died. The general detrimental effects of tagging described above would also be expected to increase mortality. J. J. Gonor (pers. comm.) who independently tagged S. purpuratus with anchor tags in the laboratory found that "... while the animals survive for months ... [they] ... eventually die sooner than non-tagged controls." Fuji (1962 and pers. comm.) kept tagged and control H. pulcherrimus in a live box for a fortnight and noted that the mortality rate of tagged urchins (0.143) was greater than that of untagged ones (0.042), although most mortality occurred within a week of tagging. Ebert (1967a) also noted that "... some mortality occurred after the

marking ... [of S. purpuratus] but after the first month mortality and tag loss could not be separated." Tag mortality recorded by Fuji and Ebert was probably far less than that suspected for Evechinus tagged with anchor tags; especially over long periods.

During recovery dives it is difficult to distinguish tagged urchins which have lost their tags from untagged urchins; hence the effects of tag loss on recovery rate remain largely unknown. However, the finding of six urchins which had lost tags from a sample of 37 apparently untagged urchins collected at marked Kaikoura sites in September 1968 suggests that tag loss may have been considerable.

The effects of tagging by anchor tags indicated by autopsied urchins in September 1968 and also the failure of tagged urchins to grow seem surprising since urchins are capable of regenerating test, spines and some internal parts (Swan, 1966). Kindred (1924) found that $1cm^2$ holes cut in the test of S. droebachiensis were closed over by a membrane and later by regenerated test plates and Ebert (1965a) found that after about two weeks a nylon loop inserted through the test of S. purpuratus was "firmly cemented in the test." On the basis of the present study and also trials of similar tags by T. A. Ebert and J. J. Gonor (pers. comm's.) it would seem that a loose mobile tag inserted through the test prevents healing around the tag insertion hole. The cause of apparent decrease in feeding rate, decrease in gonad size and sterilisation are unknown although the latter two could be related to the former (Section 10.3a). General infection or other upset of physiological processes, possibly due to the urchin's failure to completely seal the tag insertion hole, may have been responsible.

Maxwell (1957) considered that mature Evechinus migrate towards the shallower tidal zone during their summer breeding season as previously suggested for Echinus esculentus by Elmhirst (1922) and Scott (1931). But McRae (1959) who collected in the same area, did not support this opinion. At Kaikoura and Kaiteriteri, despite frequent intertidal and subtidal collecting in all seasons, no summer inshore migration was observed. Further, all Evechinus (73)

were removed from a mid-tidal pool at Kaiteriteri in late spring (3 November 1967). The pool was re-examined in mid-summer (3 January 1968) and no immigrant urchins were found; 43 new Evechinus were then placed in the pool and this was examined each month until 7 October 1968. Numbers recovered in the pool each month (Table 18) indicate that some movement from the pool may have occurred although mortality may have reduced numbers. There was certainly no influx of urchins during the breeding season.

TABLE 18 : Number of Evechinus counted in a midtidal pool at Kaiteriteri, 1968.

Date	Number	Date	Number
3 Jan	43	9 Jun	20
2 Feb	33	8 Jul	18
4 Mar	39	6 Aug	18
8 Apr	33	6 Sep	17
7 May	22	7 Oct	14

Very little movement occurred into intertidal pools cleared of Evechinus and periodically examined from 3 September 1968 to at least 6 January at Leigh, Auckland (R. T. Paine, pers. comm.).

Whether the diurnal pattern of greater movement during darkness, observed in the laboratory, is true in nature was not definitely ascertained during this study. Several observations in intertidal pools at Kaikoura suggested that this might be so; urchins, normally secretive during the day, were found in the open at night. The urchins Diadema setosum (Thornton, 1956), Centrostephanus rodgersii and Phyllacanthus parvispinus (Sinclair, 1959) were also found to be more active at night but Paracentrotus lividus was found to come up onto the tops of boulders by day (Ebling et al., 1966).

9.4 Summary

1. Newly metamorphosed Evechinus were observed in three

larval cultures 36, 30 and 28 days after fertilisation, indicating that the free-swimming larval life may last about one month. The relatively long larval life span suggests that larval dispersal may be considerable.

2. Preliminary field and laboratory tagging trials indicated that Floy Tag and Manufacturing Inc. anchor tags were suitable for marking urchins.

3. 310 Evechinus were tagged with anchor tags during late December 1967 and January 1968 at four marked sites in Third Bay Kaikoura. Tag recoveries after three, six and nine months were approximately 57%, 26% and 17%.

4. Tagged urchins were recovered only at the marked sites and only small numbers (6% at three months and 10% at six months) had moved between sites; these urchins had moved from the nearest neighbouring sites, the maximum distance between these being 4.8m.

5. 27 Evechinus were tagged in situ underwater at Kaiteriteri in October 1968. Four of these were recovered alive after one month, one at the tagging site and one at each of three positions 3m, 4m and 5m from the tagging site.

6. Gonad condition and amount of food in the gut were compared for 50 tagged and 30 untagged urchins nine months after tagging. Only five tagged urchins had gonads of normal size and appearance and only 18 could be sexed; all untagged urchins could be sexed. Mean gonad indices of tagged and untagged urchins were 0.43 and 1.12. The amount of food in the gut of tagged specimens was generally less than that of untagged specimens. Tag insertion holes were not sealed by regenerated test. No significant changes in test diameter had occurred in tagged specimens after nine months.

7. Although mortality probably accounts for most of the fall in tagged recoveries, it is considered from other evidence that the pattern indicated by tagging, of very little movement of subtidal Evechinus at Kaikoura with more at Kaiteriteri, reflects the natural situation. The amount of movement may be related to the availability of food.

8. Little movement probably occurs in intertidal

populations; there is nothing to suggest an inshore summer breeding migration.

9. Evechinus was found to move more during the night than during the day, in running seawater tanks at least.

10. REPRODUCTION

10.1 Introduction

A fairly extensive literature on echinoid reproductive biology has been reviewed by Boolootian (1966), but practically nothing has been published on Evechinus apart from McRae's (1959) note that ripe gonads could be obtained throughout most of the year except during midwinter.

The present study was aimed at understanding the general reproductive biology of Evechinus and attempting to explain differences between Kaikoura and Kaiteriteri populations. For these populations estimates were made of seasonal variations in relative gonad sizes (gonad indices) and gametogenic stages, annual volume of spawn production, size and age at maturity, and lastly, sex ratios. A possible seasonal relationship between gut and gonad size was also investigated at Kaikoura. This involved, in addition to measuring gut and gonad size, a study of seasonal changes in feeding rate.

10.2 Materials and methods

Samples of 50 similar sized Evechinus taken each month from both Kaikoura and Kaiteriteri were used to determine the reproductive cycles. Kaikoura urchins (test diameter range 9.5 to 15.0cm) were collected at Seal Reef from May 1967 to April 1968, while Kaiteriteri urchins (diameter 4.5 to 8.1cm) were collected from November 1967 to November 1968. Other samples, mentioned below, provided additional information.

The gonad condition of mature urchins was assessed from the gross appearance of intact and transversely cut gonads, from unstained smears of genital products taken mainly from the gonoducts, and by the relative gonad volume or gonad index $\left(\frac{10 \text{ gonad volume in cc}}{\text{test volume in cc}}\right)$ as originally defined by Moore (1934). Gonad volume was measured by displacement and test volume was calculated from regressions of test volume on test diameter squared

times test height (Appendix 1).

The following gametogenic condition categories were established for mature Kaikoura Evechinus by the gross appearance and gonad smears:

Females. Unripe: gonads of firm texture. These were subdivided into (a) those with a few small ova with nuclear membranes and none without, and (b) those with a larger number of ova with visible nuclear membranes and few without. Ripe: gonads of pulpy texture with at least 90% of ova without visible nuclear membranes, the ova readily extruded as a yellow granular stream on cutting the gonad and often extruded from the genital pores on handling the animals. Spent: gonads of very firm texture, thin, and with a brown fluid containing few ripe ova and much debris extruded from the gonad on cutting.

Males. Unripe: gonads of firm texture. These were subdivided into (a) those with no or few active sperm and no milt; and (b) those with many active sperm but only a small amount of milt. Ripe: gonads of pulpy texture, with large numbers of active sperm readily extruded as white milt on cutting the gonad and often extruded from the genital pores when handling the animals. Spent: gonads of very firm texture, thin, and with a brown fluid containing few sperm and sometimes a small amount of milt extruded from the gonad on cutting.

These criteria were also used to classify mature Kaiteriteri gonads. But when ripe the latter did not become as full, pulpy, or extrude such copious amounts of milt or roe as the Kaikoura gonads.

In calculating the relationship of gonad index to test size, individual gonad indices for each month, derived from the above samples were corrected to eliminate the effects of seasonal changes. This was done by adding or subtracting to each the difference between the mean gonad index for each month and a constant (the overall mean gonad index for the year). This brought the mean for each sample to a constant, the overall mean, as done by Moore et al. (1963a) for Lytechinus variegatus. Sexes were treated separately

and the data were grouped into test diameter size classes.

In deriving estimates of spawn volume, mean gonad volumes of ripe individuals were compared with those of spent individuals. The differences between these were grouped according to test diameter size classes for samples from Wakatu Point and Seal Reef, Kaikoura, and for Kaiteriteri. Only one major spawnout was evident at Kaikoura and gonad volumes of ripe specimens in January were compared with spent individuals in April. But at Kaiteriteri, 86% of the sample were ripe in December, 35% were spent in January, 86% were ripe in February and 60% were spent in March (see Fig. 19). Hence the gonad volumes of ripe December specimens were compared with spent January specimens and those of ripe February specimens were compared with spent March specimens. Data were not sufficient to treat sexes separately by size classes so that spawn outputs of males and females were compared over all size classes.

Maturity of the gonads with respect to test size and age was examined in samples from Kaikoura (July 1967) and Kaiteriteri (November 1967). Gonads were classified in a manner similar to McPherson's (1965) scheme for Tripneustes ventricosus: i.e. undeveloped, specimens with no visible, barely visible or very small transparent gonads with no recognisable sex cells; immature, specimens with small pale gonads containing no mature sex cells but with maturing sex cells apparent on microscopical examination of a gonad smear; and mature, specimens with developed gonads containing mature sex cells. The categories "undeveloped" and "immature" correspond closely with "neuter" and "developirg virgin" as defined by Fuji (1960a) for Strongylocentrotus intermedius and S. nudus.

For each monthly sample collected during investigation of the reproductive cycle at Seal Reef, Kaikoura, the gut (exclusive of the pharynx) was dissected from each urchin, washed free of its contents, drained for several minutes and weighed. Mean gut indices were calculated from the formula,

$$\text{gut index} = \frac{100. \text{ wet weight of gut in gm}}{\text{test volume in cc}}$$

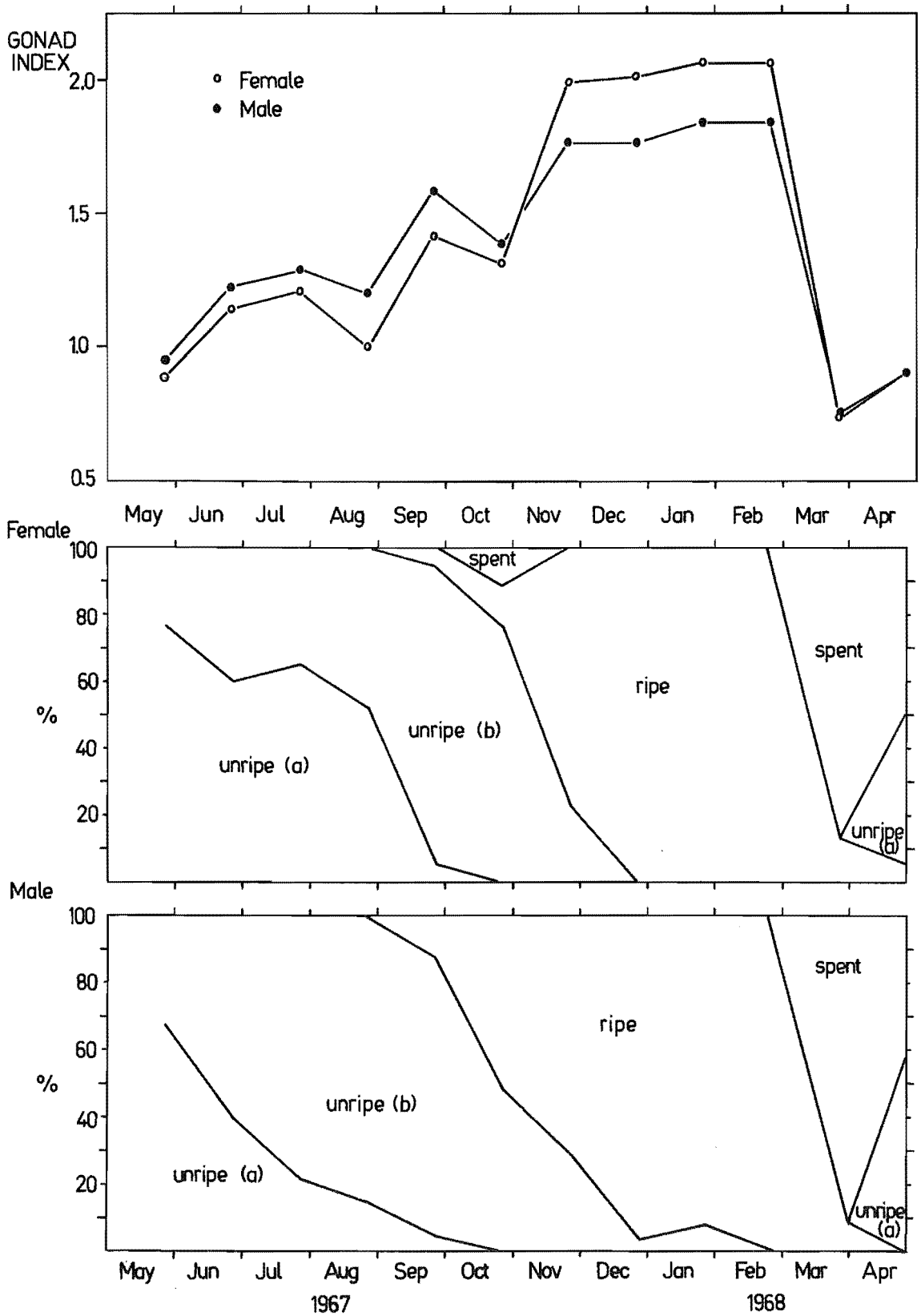

GONAD INDEX
2.0
1.5
1.0
0.5
Female
Male
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
Female
100
80
60
40
20
%
spent
ripe
unripe (b)
unripe (a)
spent
unripe (a)
Male
100
80
60
40
20
%
ripe
unripe (b)
unripe (a)
spent
unripe (a)
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
1967
1968

Figure 16

Seasonal variation in mean gonad indices of mature male and female Evechinus at Seal Reef, Kaikoura, 1967-68.

Figure 17

Gametogenic cycles of mature female and male Evechinus at Seal Reef, Kaikoura, 1967-68.

Laboratory observations on feeding rates were made each month with 10 similar sized urchins collected from St Kilda Rocks at Kaikoura from July 1968 to March 1969. Experiments were carried out in a 9.4 cu.ft aquarium equally divided by a partition. A flow of unfiltered running seawater into two opposite corners of the aquarium was maintained at about 4 gallons per minute; this was sufficient to create a steady circulation of water. The brown alga Lessonia variegata was used as food and prior to the feeding rate measurements five urchins were kept in each half of the aquarium with abundant food for one week. The alga was then removed and 15 strips (6 x 2cm) of fresh Lessonia (3 per urchin) were blotted, weighed and placed with each group of five urchins. Two days later the alga was removed, blotted and weighed. All urchins were then placed in one half of the aquarium and were provided with 30 weighed strips of Lessonia. Algal consumption in terms of grams per urchin per day was again noted after two days. The urchins were then measured, weighed and dissected for determination of gonad condition (gametogenic stage and gonad index).

10.3 Results and Discussion

In the present discussion the seasons include the following months: summer - December, January, February; autumn - March, April, May; winter - June, July, August; and spring - September, October, November.

10.3a Annual reproductive cycles

i. Seasonal variation in gonad index. Spawn output.

Seasonal variations in the gonad indices of male and female Evechinus at Kaikoura and Kaiteriteri are shown in Figures 16, 31 and 18. The gonad indices of Seal Reef Evechinus tended to increase throughout the winter and spring and showed a sharp increase in late spring and early summer to reach a midsummer maximum in January. After maintaining their maxima (2.07 in females and 1.84 in males) during January and February, a marked fall to 0.74 was observed in March (Fig. 16). An essentially similar pattern was observed in the following year (1968-'69) at St Kilda

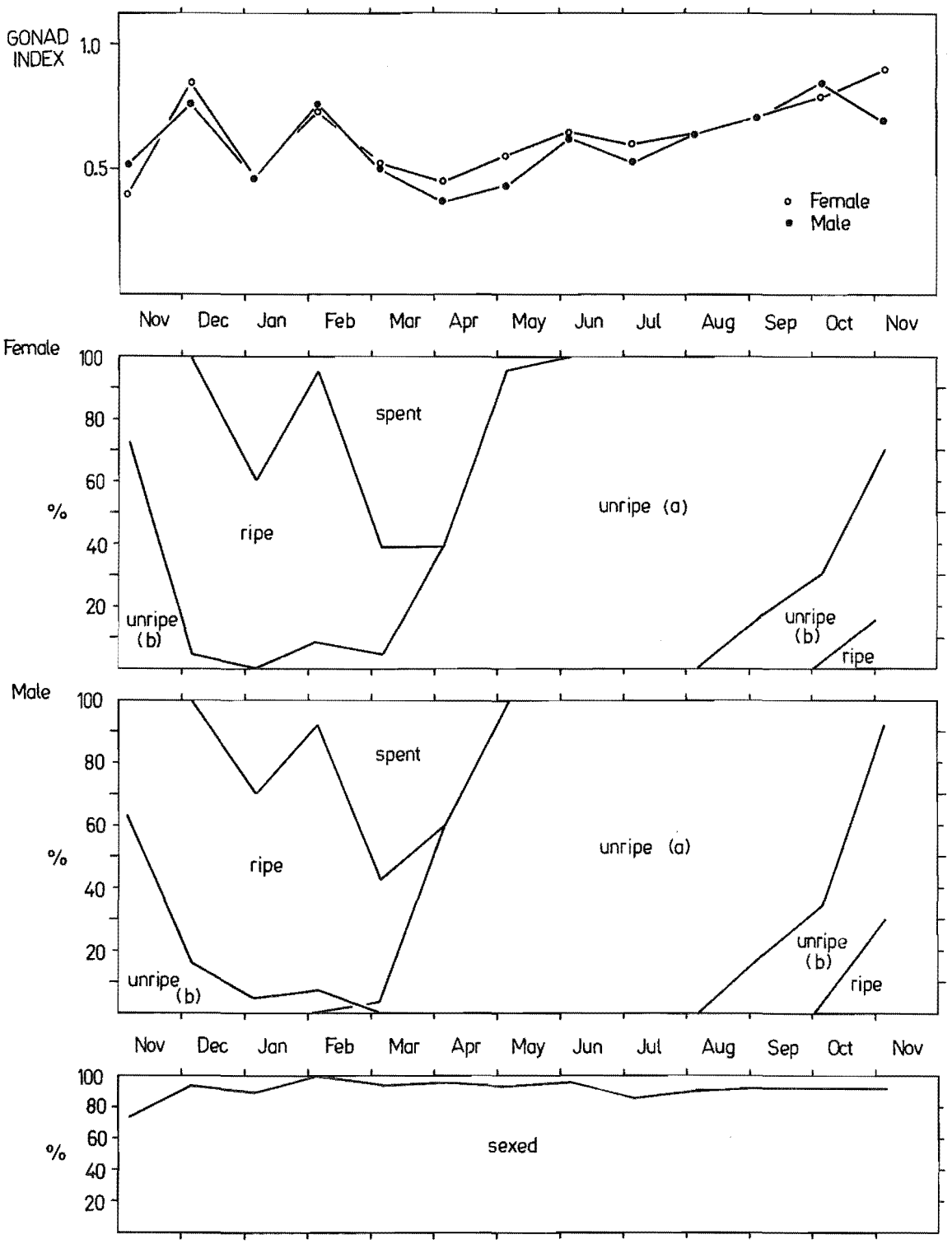

GONAD INDEX
1.0
0.5
Female
Male
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Female
100
80
60
40
20
%
spent
ripe
unripe (a)
unripe (b)
unripe (b)
ripe
Male
100
80
60
40
20
%
spent
ripe
unripe (a)
unripe (b)
unripe (b)
ripe
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
100
80
60
40
20
%
sexed

Figure 18

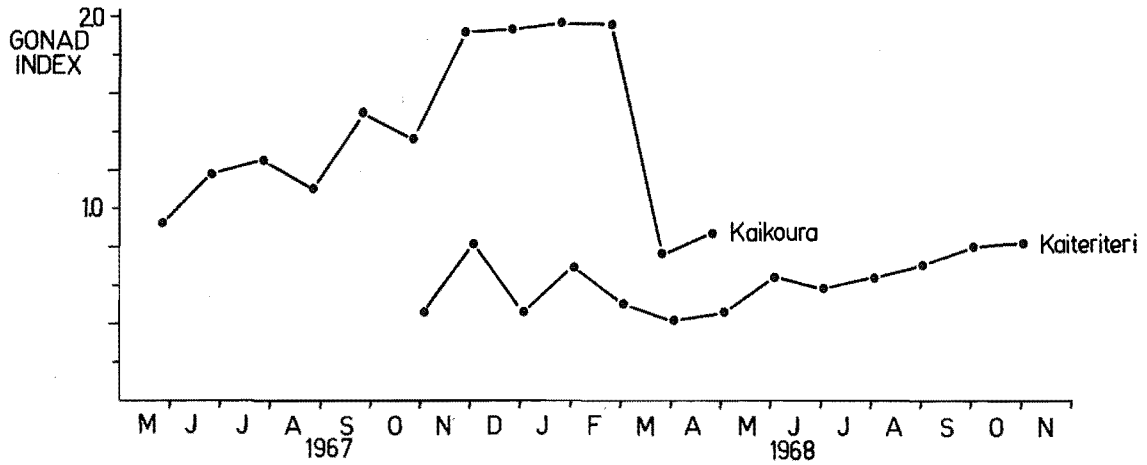
Seasonal variation in mean gonad indices of mature male and female Evechinus at Kaiteriteri, 1967-68.

Figure 19

Gametogenic cycles of mature female and male Evechinus at Kaiteriteri, 1967-68.

Figure 20

Percentage of mature Evechinus able to be sexed at Kaiteriteri, 1967-68.


GONAD INDEX
2.0
1.0
Kaikoura
Kaiteriteri
M J J A S O N D J F M A M J J A S O N
1967
1968

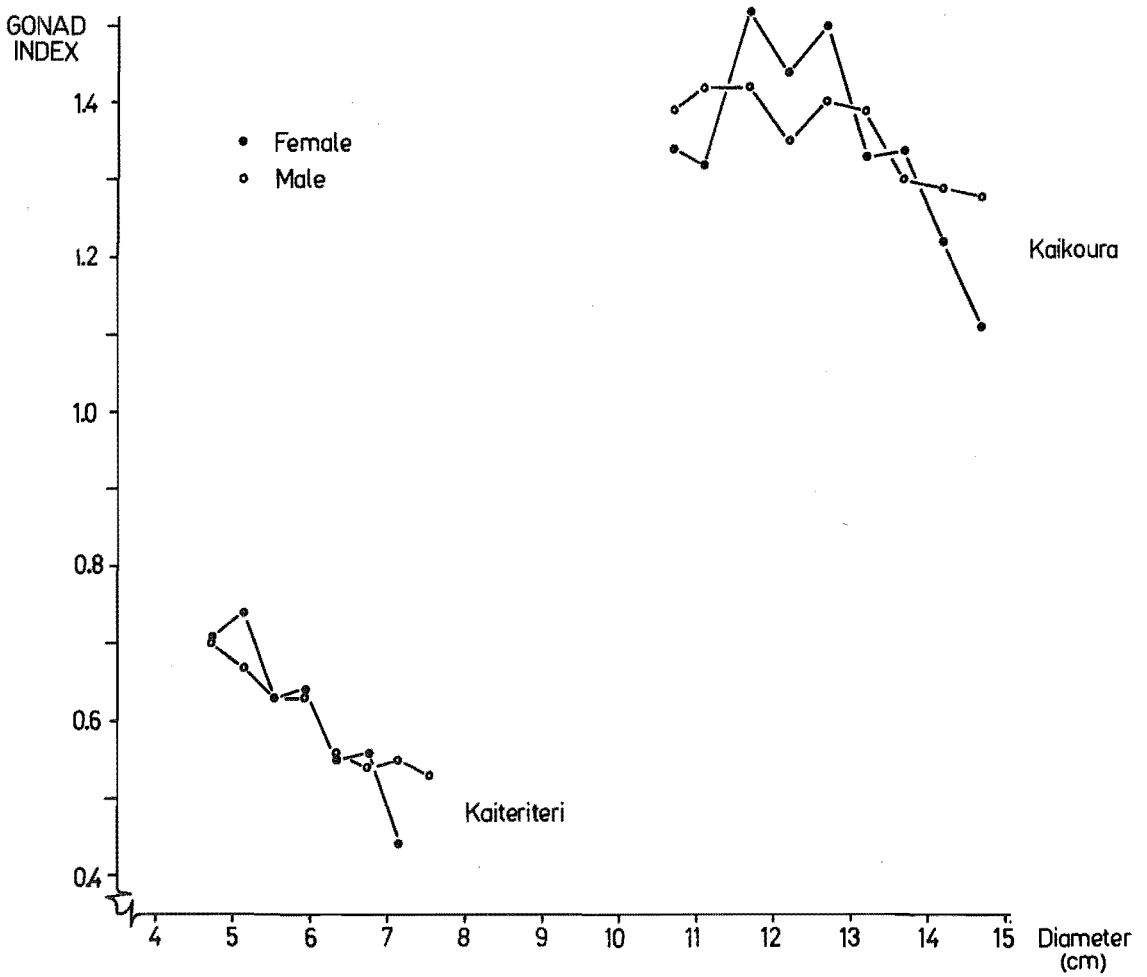

GONAD INDEX
1.4
1.2
1.0
0.8
0.6
0.4
Female
Male
Kaikoura
Kaiteriteri
4 5 6 7 8 9 10 11 12 13 14 15
Diameter (cm)

Figure 21

Comparison of Kaikoura and Kaiteriteri mean gonad indices (sexes combined), 1967-68.

Figure 22

Gonad index with respect to test size for male and female Evechinus at Kaikoura and Kaiteriteri. For explanation see text.

Rocks, although the sharp fall in gonad index was observed in late February (Fig. 31).

At Kaiteriteri similar increases in gonad indices occurred during the winter and spring but two maxima were observed during the summer. The second was followed by a decline in March to a minimum of 0.46 in females and 0.38 in males in April. Higher gonad indices were recorded in November 1968 than in November 1967 (Fig. 18).

The cycles of gonad indices differed at the two localities. Firstly, the gonad indices were higher at Kaikoura. Secondly, only one summer peak was found at Kaikoura but two were present at Kaiteriteri, and finally, the relationship of male to female gonad indices was simpler at Kaikoura.

Seasonal variations in gonad indices (sexes combined) are compared in Figure 21 for Seal Reef, Kaikoura, and Kaiteriteri. The maximum mean Kaiteriteri gonad index was just higher than the minimum at Kaikoura despite the fact that Kaikoura urchins were larger. The differences in gonad indices are also shown in Figure 22 which also implies that the absolute size of Kaiteriteri gonads was much smaller. Other data showed that the absolute size of Kaiteriteri gonads ranged from 0.5 to 22.0cc while that of Kaikoura gonads ranged from 20.0 to 257cc over the size ranges indicated in Figure 22.

Spawn production was also greater at Kaikoura. Estimates of minimum spawn production in cc with respect to test size at two Kaikoura localities (Fig. 29) ranged from 20.8 to 80.5cc. These contrast with the Kaiteriteri samples (Table 20). Although data were not sufficient to indicate a clear trend in Kaiteriteri production with respect to test size, mean production based on comparisons of spent January specimens with ripe December specimens was 4.6cc and that based on spent March and ripe February specimens was 5.1cc. The above estimates are probably minimal since fractional spawning has been suggested at least for Kaikoura urchins (Section 10.3a ii). Moore et al. (1963a) gave estimates of minimum annual spawn production ranging from ca 10 to 16cc for Lytechinus variegatus of similar test size to Kaiteriteri Evechinus.

Differences in the gonad indices, and presumably production, of urchin species living in different habitats have also been shown for Echinus esculentus (Moore, 1934, 1937), Strongylocentrotus purpuratus (Lasker and Giese, 1954; Boolootian, 1960; Ebert, 1968) and S. intermedius (Fuji, 1960c; Kawamura, 1964, 1965; Kawamura and Taki, 1965). In most cases lower gonad indices were correlated with habitats having smaller amounts of food although Boolootian (1960) suggested that temperature might be significant. Although temperatures were higher at Kaiteriteri than at Kaikoura (Fig. 2), Evechinus with gonads larger than those at Kaiteriteri were found in warmer waters further north, suggesting that temperature differences were not significant. Kaiteriteri has a much more impoverished algal flora than Kaikoura (Section 1.1) and this is probably the main factor influencing gonad size and production. Support for this statement was gained from observations on urchins in neighbouring areas in the Marlborough Sounds, some areas with abundant algae and others without. Urchins in barren areas invariably had small gonads while those in nearby weeded areas had large gonads. Further, the effects of food supply on gonad growth were studied in aquaria. Samples of 20 Kaiteriteri Evechinus were starved (except for detritus and microscopic growth) and 20 were fed on a variety of algae for six months in running seawater aquaria at Kaikoura. After six months the gonads of all starved specimens were undeveloped very thin threads with volume and thus gonad index approaching zero. Fed specimens showed greater gonad development with a mean gonad index of 0.39. Similar observations have been cited for other echinoderms by Boolootian (1966).

Gonad indices of female Kaikoura Evechinus were consistently lower during the winter and spring and consistently higher during the summer than those of males (Fig. 16 and Table 19) although some exceptions occurred (Fig. 25). This relationship itself indicates that the spawn output of females was volumetrically larger than that of males. Such a systematic trend was not evident at Kaiteriteri. Minimum estimates of the spawn output of male and female Kaikoura and Kaiteriteri Evechinus (Table 20) indicate that

females spawned larger volumes than males at both localities but that this difference was greater at Kaikoura.

TABLE 19 : Gonad indices at Wakatu Point, Kaikoura, 1967-'68.

Date	Gonad index Female	Male
July '67	1.30	1.46
October '67	1.82	1.90
January '68	1.99	1.81
April '68	0.91	0.98

TABLE 20 : Estimates of minimum spawn production of male and female Evechinus at Seal Reef (February-March 1968) and Kaiteriteri (1967-'68) *

Locality	Sex	Mean gonad volume (cc) Ripe	Spent	Difference (= output)
Kaikoura	Female	142.9 (23)	54.9 (26)	88.0
	Male	124.9 (27)	58.2 (24)	66.7
$Kaiteriteri_1$	Female	7.0 (22)	2.0 (10)	5.0
	Male	7.7 (18)	3.5 (6)	4.2
$Kaiteriteri_2$	Female	9.14(22)	4.00(14)	5.14
	Male	9.41(18)	4.29(14)	5.12

* Sample sizes shown in parentheses.
$Kaiteriteri_1$, December 1967 and January 1968;
$Kaiteriteri_2$, February and March 1968.

Larger spawn volumes in females than males may be characteristic of urchins. Moore et al. (1963a) found that the spawn output

of female L. variegatus was 36% greater than that of males while from Fuji (1960a) ratios of full to empty gonads in S. intermedius were 4.4 in males and 5.5 in females. The mean gonad volume of the heart urchin Moira atrops was 15% higher in females (Moore and Lopez, 1966).

ii. Gametogenic cycle and spawning season

Percentages of the different gametogenic stages at Kaikoura and Kaiteriteri for each month (Figs. 17, 19 and 23) show that cycles at both localities are clearly annual. They are similar in that they show progressional development from the unripe (a) to the unripe (b) condition throughout the late autumn, winter and spring to the ripe condition in late spring and early summer. Most animals were ripe throughout the summer and largest numbers of spent individuals were found in early autumn. However, some differences are evident in the gametogenic cycles.

Firstly, the unripe (a) condition in both males and females extended over a greater part of the year at Kaiteriteri than at Kaikoura. Secondly, ripeness in males preceded that in females at Kaikoura but did not appear to do so at Kaiteriteri, and finally, more variation was found in gametogenic stages during summer at Kaiteriteri; a considerable number of spent individuals (40% females and 30% males) was found in midsummer at Kaiteriteri but not at Kaikoura.

Not only did Kaiteriteri Evechinus show the unripe (a) condition for a greater part of the year, but a small percentage were also unable to be sexed at all parts of the year (Fig. 20). These generally had very thin, dark brown gonads contrasting with the light brown, orange or yellow gonad of the other urchins. H. B. Moore (pers. comm.) has also encountered similar small gonads in urchin samples. In contrast, mature Kaikoura urchins could be sexed during any month of the year and males generally had at least a small number of active sperm. From figures given in Moore (1934) it can be seen that a population of Echinus esculentus which showed lower gonad indices was also unripe for a longer period than a

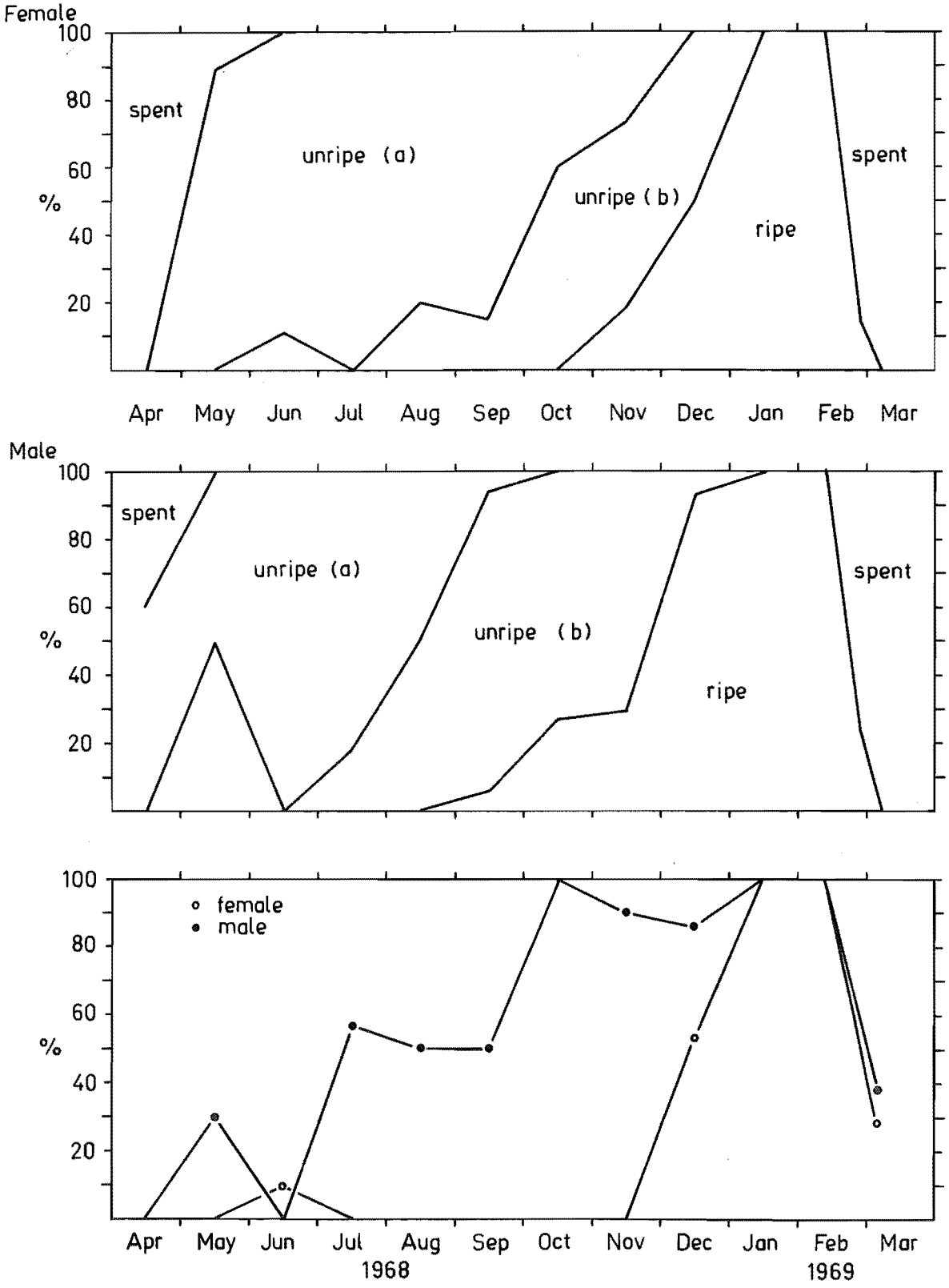

Female
100
80
60
40
20
%
spent
unripe (a)
unripe (b)
ripe
spent
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Male
100
80
60
40
20
%
spent
unripe (a)
unripe (b)
ripe
spent
100
80
60
40
20
%
female
male
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
1968
1969

Figure 23

Gametogenic cycles of male and female Evechinus at St Kilda Rocks, Kaikoura, 1968-69.

Figure 24

Percentages of female and male Evechinus induced to spawn on injection of 0.5M KCl at St Kilda Rocks, Kaikoura, 1968-69.

population with higher gonad indices.

Since some (usually large) urchins with very thin dark brown gonads were found at all times at Kaiteriteri, it is unlikely that they were seasonally spent. Similarly, very large Kaikoura urchins often had relatively small and dark gonads, although these generally contained apparently healthy genital products. Decreasing gonad index with increasing urchin size is evident at both Kaikoura and Kaiteriteri (Fig. 22). These observations might indicate that Evechinus becomes reproductively senile and that this condition is more evident at Kaiteriteri than Kaikoura. Reproductive senility has also been suggested for the sea star Asterias rubens and the heart urchin Brissopsis lyrifera (Thorson, 1946 and Mortensen, 1920; both cited by Swan, 1966).

The ripening of males before females has been recorded for the urchins Echinus esculentus (Moore, 1934), Strongylocentrotus purpuratus, S. franciscanus (Bennet and Giese, 1955), S. intermedius and S. nudus (Fuji, 1960c). A similar pattern was found for Evechinus at Kaikoura during 1967 and 1968 (Figs. 17, 23 and 24). Gonad condition was examined during both years and forced shedding experiments were tried during 1968, using Tyler's (1949) method of injecting 0.5M KCl. These experiments showed that males were capable of ejecting ripe gametes earlier in the year than females (Fig. 24). At Kaiteriteri, male ripeness did not appear to precede female ripeness (Fig. 19) but this may be more apparent than real. Under the gametogenic classification system, unripe (b) specimens had a small amount of milt. But ripe males at Kaiteriteri always exuded less copious amounts than those at Kaikoura, and thus some specimens classified as 'unripe (b)' could have been ripe.

Both spent and ripe urchins were found in January and March 1968 at Kaiteriteri indicating that more than one major spawning occurred. In contrast, the gonad index and gametogenic cycles at Kaikoura (Figs. 16, 17, 23, 31) indicated only one major spawning each summer, even though ripe and fertilisable gametes were present throughout the late spring and early summer. Moore et al. (1963a), however, assumed that some spawning occurred in Lytechinus variegatus throughout the period when ripe gametes were present and

Booloctian (1966) defined breeding season in echinoderms as "the time when mature, fertilisable gametes are present". Thus it was decided to test the following hypotheses: (a) "does fractional spawning occur in Kaikoura Evechinus throughout the summer;" or, (b) "does only one major spawning occur?"

To test whether fractional spawning occurred and also to investigate environmental influences on breeding, samples of 35 to 40 urchins were taken at three day intervals from an aggregation occupying ca 12m^2 at Sharks Tooth Point from 30 December 1968 to 5 February 1969. Sea conditions and temperature were noted at each collection. Within a few hours of sampling, each urchin was inverted over a beaker of seawater and injected with 5ml of 0.5M KCl to see whether spawning could be induced; the amount of induced spawn was scored on a 0 to 4 scale. The urchins were then sexed and gonad condition was assessed from gonad indices, gross appearance and sometimes gonad smears. Mean gonad indices, phases of the moon, percentages induced to spawn, mean scores of the amount of induced spawn, and sea temperatures are shown in Figures 25, 26 and 27.

Although, with few exceptions, all urchins were ripe over the sampling period, gonad indices, percentages induced to spawn and amounts of induced spawn did not remain uniform over the sampling period indicating that the gonad state changed. A gradual decline followed by a fairly rapid rise separated peaks in gonad indices, at 2 and 29 January. Percentages induced to spawn remained high ($>80\%$) over the sampling period but showed a decline near the end of January. A similar decline occurred in the amount of induced spawn and a brief peak occurred in both in early February.

Considered alone, the two peaks in gonad indices suggest that two spawnings occurred during the sampling period. But if the induced spawn amounts and percentages reflect the degree of gonad ripeness it would be expected that these would increase as gonads reached peak ripeness, then decrease after spawning. However, little change occurred in these after the first gonad index peak although slight falls might indicate that a few animals partially

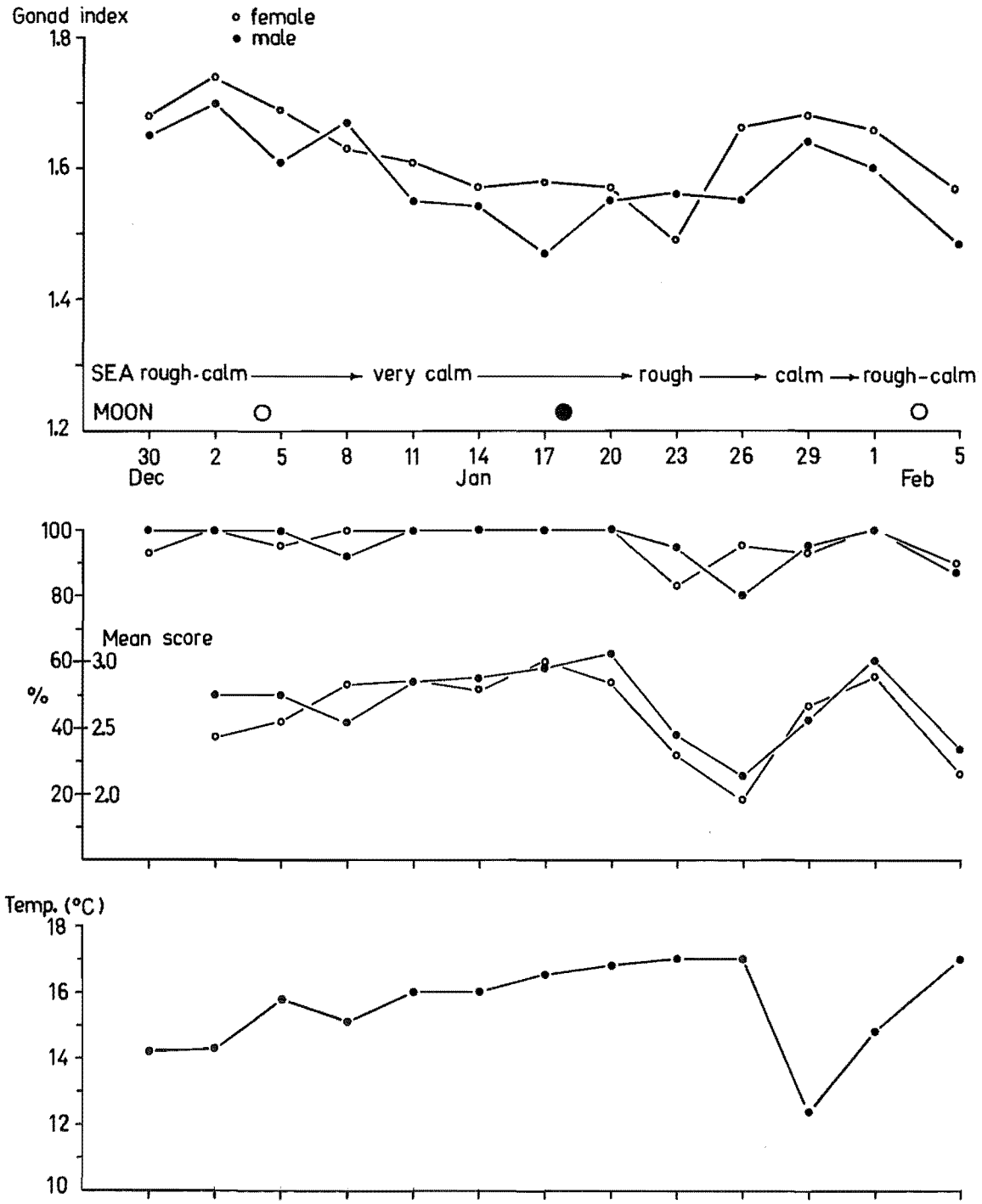

Gonad index
female
male
1.8
1.6
1.4
1.2
SEA rough-calm
very calm
rough
calm
rough-calm
MOON
30 Dec
2
5
8
11
14 Jan
17
20
23
26
29
1
5 Feb
100
80
60
40
20
%
Mean score
3.0
2.5
2.0
Temp. (°C)
18
16
14
12
10

Figure 25

Mean gonad indices of female and male Evechinus at Sharks Tooth Point, Kaikoura, December 1968 to February 1969. Sea conditions and moon phases are also shown.

Figure 26

Percentages of female and male Evechinus induced to spawn and mean scores of the amount of spawn at Sharks Tooth Point.

Figure 27

Sea temperatures at Sharks Tooth Point, December 1968 to February 1969.

spawned. Increases to peaks followed by decreases, which indicate spawning, occurred in late January and early February. Similar changes occurred in the number of animals which spawned simultaneously when inverted over beakers of seawater (Table 21). Only a small drop in female gonad index occurred at the first decrease but a greater fall in male and female gonad indices occurred at the second.

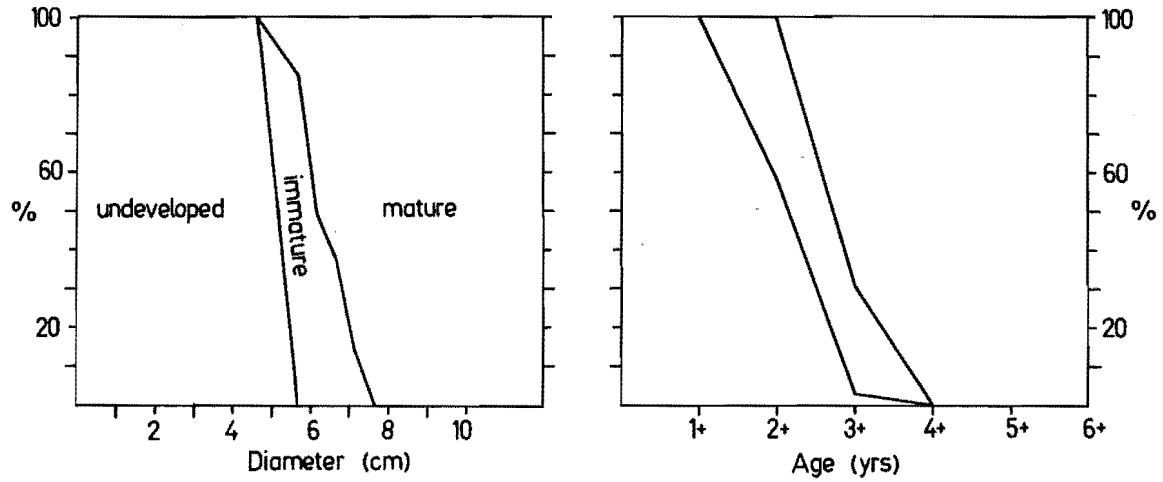
TABLE 21 : Number of Evechinus spawning without injection, 1969. Observations were made for only part of the sampling period.

Sample	Date	Number spawning	Percentage spawning
8	20 Jan.	15	43
9	23 Jan.	2	6
10	26 Jan.	4	12
11	29 Jan.	16	46
12	1 Feb.	6	17
13	5 Feb.	8	23

Further, the gross appearance of gonads after the second peak suggested that many were partially spent; but the appearance of those after the first differed little from that of fully ripe gonads. These indicate that the second spawning was more extensive than the first. That spawning can occur without large change in gonad index was indicated from a sample which was kept for two days in the laboratory. Fifteen males, from the sample which contained 29 males, were dissected on 16 January 1968. That night most (or all) of the remaining males spawned spontaneously in quantities which clouded the water of the 100 gallon running seawater tank in which they were. These males were dissected the next morning. Only a slight change in gonad index occurred (from 1.86 to 1.76) and this was not statistically significant ($t = 1.04$; $P = 0.15$).

Throughout the sampling period almost all animals had consider-

KAIKOURA



SIZE AGE

KAITERITERI

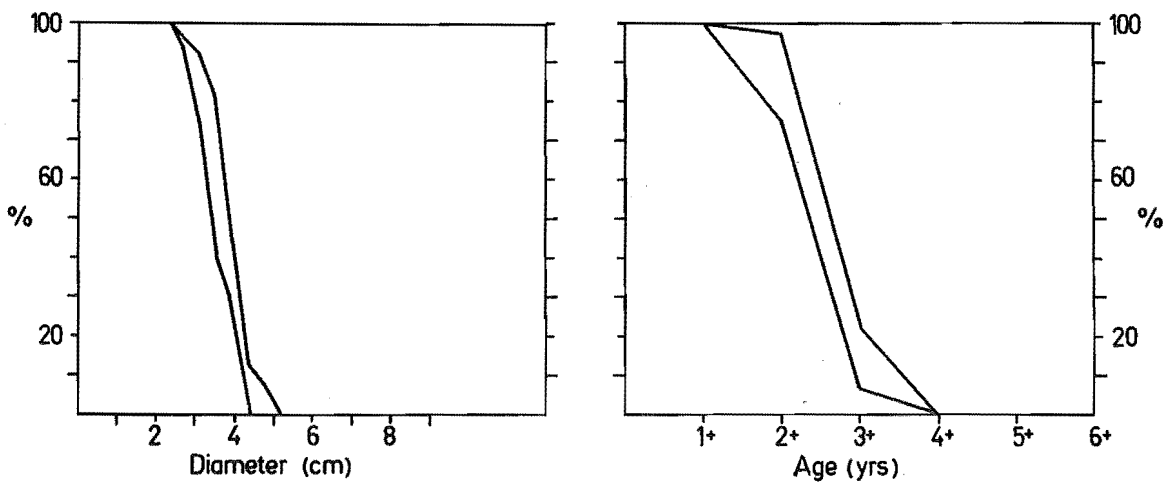


Figure 28

Maturity of Evechinus with respect to size and age (sexes combined) at Kaikoura (July 1967) and Kaiteriteri (November 1967).

able quantities of ripe gametes which could be successfully fertilised. This, together with the relatively small changes in gonad indices (c.f. Figs. 16 and 31) indicate that any spawning was fractional rather than complete.

The following observations substantiate fractional spawning in Kaikoura Evechinus: (a) successful fertilisations were performed throughout the summers of 1967 to 1969; (b) individuals spawned spontaneously in running seawater tanks at Kaikoura on 16 January (midsummer) and 1 March (early autumn) 1968 and these urchins did not become completely spent; and (c) diameter frequency distributions of eggs in gonad smears from four urchins examined in December 1968 and January 1969 were bimodal with modes at 60μ (developing eggs) and 130μ (fully ripe eggs). This could indicate that two generations of eggs were present as Pearse and Phillips (1968) found in Echinometra mathaei although in fishes, at least, multimodal egg size distributions do not always indicate fractional spawning (Nikolsky, 1963).

The breeding season at Kaikoura might thus be regarded as extending mainly over the three summer months although major spawning occurred in late summer and early autumn as indicated by the sharp fall in gonad indices and appearance of completely spent individuals at Seal Reef (Figs. 16 and 17) and St Kilda Rocks (Figs. 23 and 31). In the latter area a fall in gonad index from 1.85 to 1.00 occurred in samples separated only by 13 days in late February 1969. That major spawning occurs in late summer or early autumn was also indicated by plankton samples which were made weekly in December 1967 and January 1968, bi-weekly in early February, more frequently in late February and March, and weekly in April. Although large numbers of Evechinus plutei were never found, a few were obtained on 29 February, 3 March, 5 March, 7 March and 15 March 1968, the largest number being collected on the last date.

Little can be concluded about the factors influencing spawning from the Sharks Tooth Point study. Peaks in gonad indices just preceded full moon in both January and February (Fig. 25) and this

might be considered as evidence for lunar periodicity (Kobayashi, 1967; Moore et al., 1963a). But little, if any, spawning appeared to occur at full moon in January while spawning appeared to occur nearly two weeks before full moon as well as at full moon in February. Further, the urchins were subjected to a marked rise in temperature at this time (Fig. 27) and this may have stimulated spawning. Over most of January seas were very calm (Fig. 25) and very little drift algae was present at the sampling site. Relatively large amounts of substrate with little macroscopic algae was found in the gut of urchins over this period. Food quantity has been found to influence gonad size in urchins (Section 10.3a) and it is possible that the urchins sampled were utilising food reserves stored in the gonad over the calm spell, thus reducing the gonad size. When seas became rough (22 January) urchins began feeding extensively on drift algae. This may have then resulted in an increase in gonad size. Kobayashi (1967) suggested that the spawning of the urchin Mespila globulus "... seemed to be hastened by rough water ..." It is interesting that the suggested late January Evechinus spawning coincided with the end of calm seas.

10.3b Size and age at maturity

Percentage frequency distributions of undeveloped, immature and mature Evechinus with respect to test size and age at Kaikoura and Kaiteriteri (Fig. 28) indicate that urchins at Kaiteriteri first mature at a smaller size (ca 3.5 to 4.5 cm) than do those at Kaikoura (ca 5.5 to 7.5 cm). However, age at maturity was similar in both areas, Evechinus first maturing in its third and fourth years. Although the Kaikoura sample was taken earlier in the year than that from Kaiteriteri (July as compared with November) it is considered that the difference did not significantly affect the above conclusions. Some of the immature Kaikoura urchins probably matured between July and November but during this interval these would also have grown; they would thus have little altered the size at maturity relationship.

Detailed information on the size and age at maturity is not

extensive for echinoids. McPherson (1965) gave data on size at maturity for Tripneustes ventricosus as did Fuji (1960b) and Kawamura (1964 and pers. comm.) for Strongylocentrotus intermedius. Kawamura found that one year urchins may mature where food was very plentiful but that one and two year urchins could remain immature where food was limiting. Three year old urchins were mature in all the localities he studied. Moore (1936) found that Echinocardium cordatum first spawned in its second year but Buchanan (1966) found that maturity may be deferred in some populations. It has been suggested (Moore, 1966) that "where food is scarce, animals may go through their main growing phase before diverting energy to gonad production" (i.e. mature when older). It would appear that food limitation at Kaiteriteri is not sufficient to suppress the formation and maturity of gonads but is sufficient to restrict their size (Section 10.3a).

10.3c Sex ratio

Sex ratios of mature Evechinus did not differ significantly from 1:1 at Kaiteriteri, Sharks Tooth Point and in a series of samples from other Kaikoura localities (Table 22). But significantly more males than females were found at Seal Reef, Nine Pins, St Kilda Rocks and also for all Kaikoura samples combined. Sex ratios in urchins generally approximate one (Harvey, 1956; Fuji, 1960b; Moore et al., 1963a) although McPherson (1965) found more females than males among larger Tripneustes ventricosus; in smaller specimens the sex ratio was about one. McPherson suggested that either differential growth or mortality, or hermaphroditism might be involved. Seasonal changes in sex ratios have been noted in some echinoderms (Reverberi, 1940, 1947; Neefs, 1952, 1953; both cited by Delavault, 1966).

Little can be said regarding the sex ratios of different Evechinus populations, particularly the preponderance of males. There is no reason to suspect sampling bias since at Kaikoura, at least, sexes are randomly distributed in clumps (Section 2.4a) and samples consisted of all or most individuals from clumps, or were

TABLE 22 : Sex compositions of mature Evechinus populations

Date	Locality	N	female	male	female/male	X^2	P
1967-68	Kaiteriteri[1]	550	270	280	0.96	0.18	$0.75 > P > 0.50$
Jan.'69	Sharks Tooth Point[2]	470	233	237	0.98	0.03	$P \simeq 0.90$
1967-68	Kaikoura[3]	284	137	147	0.93	0.35	$0.75 > P > 0.50$
1967-68	Seal Reef[4]	596	273	323	0.85	4.19	$0.05 > P > 0.025$
Nov.'68	Nine Pins[5]	306	175	131	0.75	6.30	$P < 0.005$
Jul.'68	St Kilda Rocks[6]	404	167	237	0.70	12.0	$P < 0.005$
1967-68	Total Kaikoura	2060	985	1075	0.92	3.95	$0.05 > P > 0.025$

Notes: 1: ca 50 per month in one area; 2: nearly all of a large aggregation; 3: various localities, quadrat samples; 4: 50 per month from several aggregations; 5: most of two neighbouring aggregations; 6: quadrat samples from several aggregations.

taken from within quadrats; further, samples were not small.

In the Seal Reef population, at least, there was no marked seasonal change in sex ratio (Table 23).

TABLE 23 : Sex composition of Seal Reef Evechinus, May 1967 to April 1968.

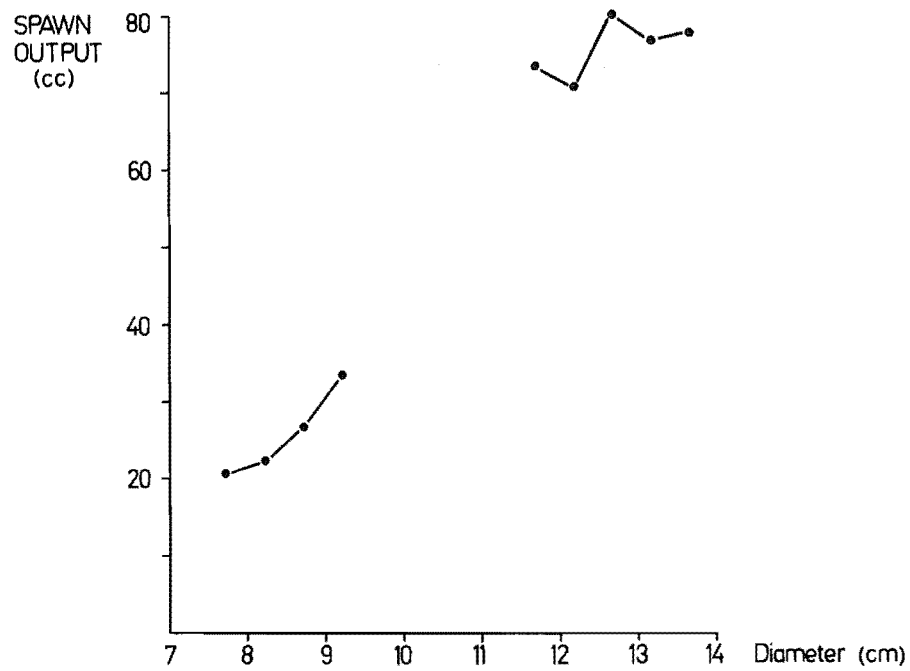
Months	Female	Male	% female
May - Jun.	45	53	46
Jul. - Aug.	42	56	43
Sep. - Oct.	48	52	48
Nov. - Dec.	43	57	43
Jan. - Feb.	49	51	49
Mar. - Apr.	46	54	46

Most individuals in the above samples were large (>10.0cm diameter at Kaikoura; > 5.0cm diameter at Kaiteriteri) but although data were not extensive, there was no evident change in sex ratio with size, at least in the St Kilda Rocks sample (Table 24).

TABLE 24 : Evechinus sex composition with respect to test size at St Kilda Rocks, July 1968.

Test diameter (cm)	Female	Male	% female
7.0 - 8.9	10	15	40
9.0 - 10.9	38	64	37
11.0 - 12.9	44	69	39

More intensive sampling, particularly of newly matured animals, together with consideration of factors involved in the survival of sexes would be necessary to determine whether differential mortality is responsible for unequal sex ratios in Evechinus. Hermaphroditism


SPAWN
OUTPUT
(cc)
80
60
40
20
7
8
9
10
11
12
13
14
Diameter (cm)

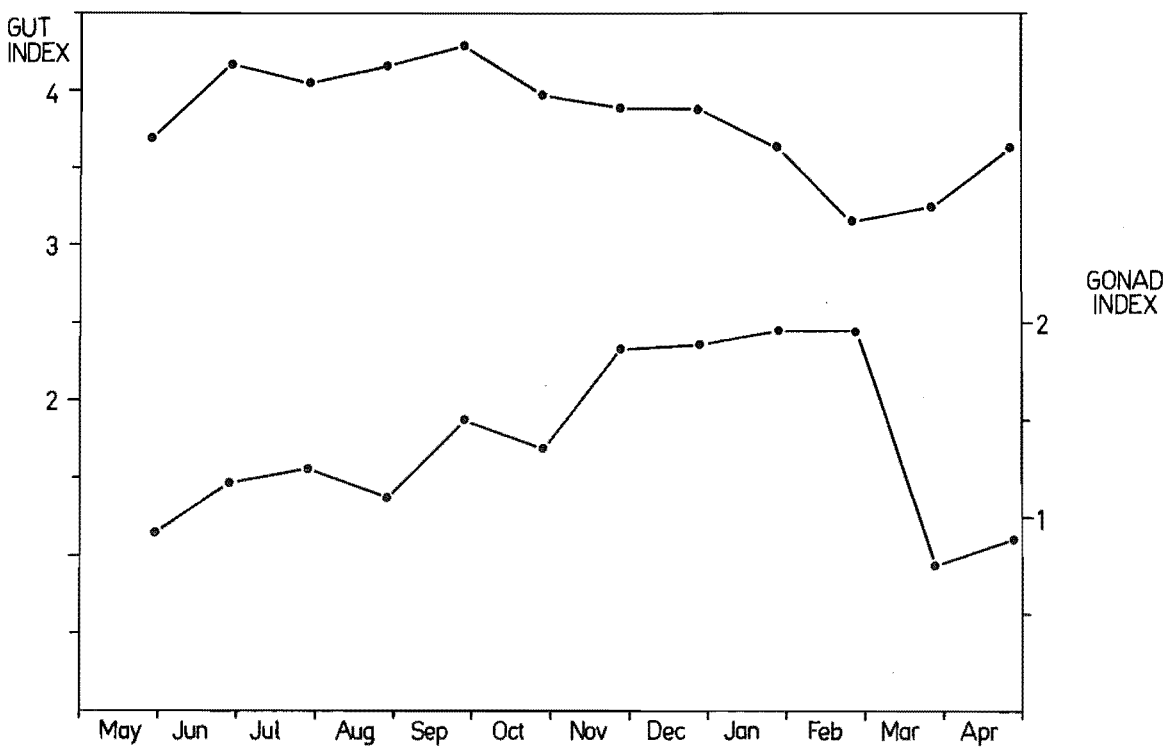

GUT
INDEX
4
3
2
GONAD
INDEX
2
1
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr

Figure 29

Estimates of minimum spawn output for summer 1967-68 at Wakatu Point and Seal Reef, Kaikoura.

Figure 30

Mean gut and gonad indices (sexes combined) for Evechinus at Seal Reef, Kaikoura, 1967-68.

is unlikely to be involved since no hermaphrodites were observed and, except under exceptional circumstances, hermaphroditism is rare in echinoids (Moore et al., 1963a and b).

10.3d Seasonal changes in the relative gut size and feeding rate of Kaikoura Evechinus

As with the gonad, an annual cycle in gut size was apparent at Seal Reef (Fig. 30) but the two were out of phase, the gut index being maximum in early spring when the gonad was increasing in size after spawning and minimum in late summer when the gonad index was maximum. A very similar relationship to that between gut and gonad in Evechinus was found between hepatic gland and gonad in the sea stars Pisaster ochraceus and P. brevispinus (Farmanfarmaian et al., 1958). Lawrence, Lawrence and Holland (1965) found that the gonad cycle of Strongylocentrotus purpuratus also lagged behind that of the gut.

It is well established that the hepatic glands of sea stars act as food storage organs (Anderson, 1966) and recent evidence suggests that the gut walls in echinoids as well as the gonads serve a similar function (Anderson, 1966; Fuji, 1961; Lawrence, Lawrence and Giese, 1966). That this is so in Evechinus was suggested by comparison of the gut indices of fed and starved animals. Samples of 40 Evechinus from Kaiteriteri and 36 from Kaikoura were kept in two running seawater tanks at Kaikoura from April to October 1968. The tanks were equally divided into two to separate half of each sample of urchins, which were fed on a frequently renewed mixed algal diet, from the other halves which were starved except for detritus and microscopic growth. After six months, the gut indices of fed specimens were significantly higher than those of starved (Table 25).

Given that the gut walls and gonads in Evechinus function as food stores, the observed relationship between gut and gonad might indicate that during the winter when gonads are developing slowly, a food excess is available for storage in the gut walls, resulting in an increase in gut weight. During the spring and summer,

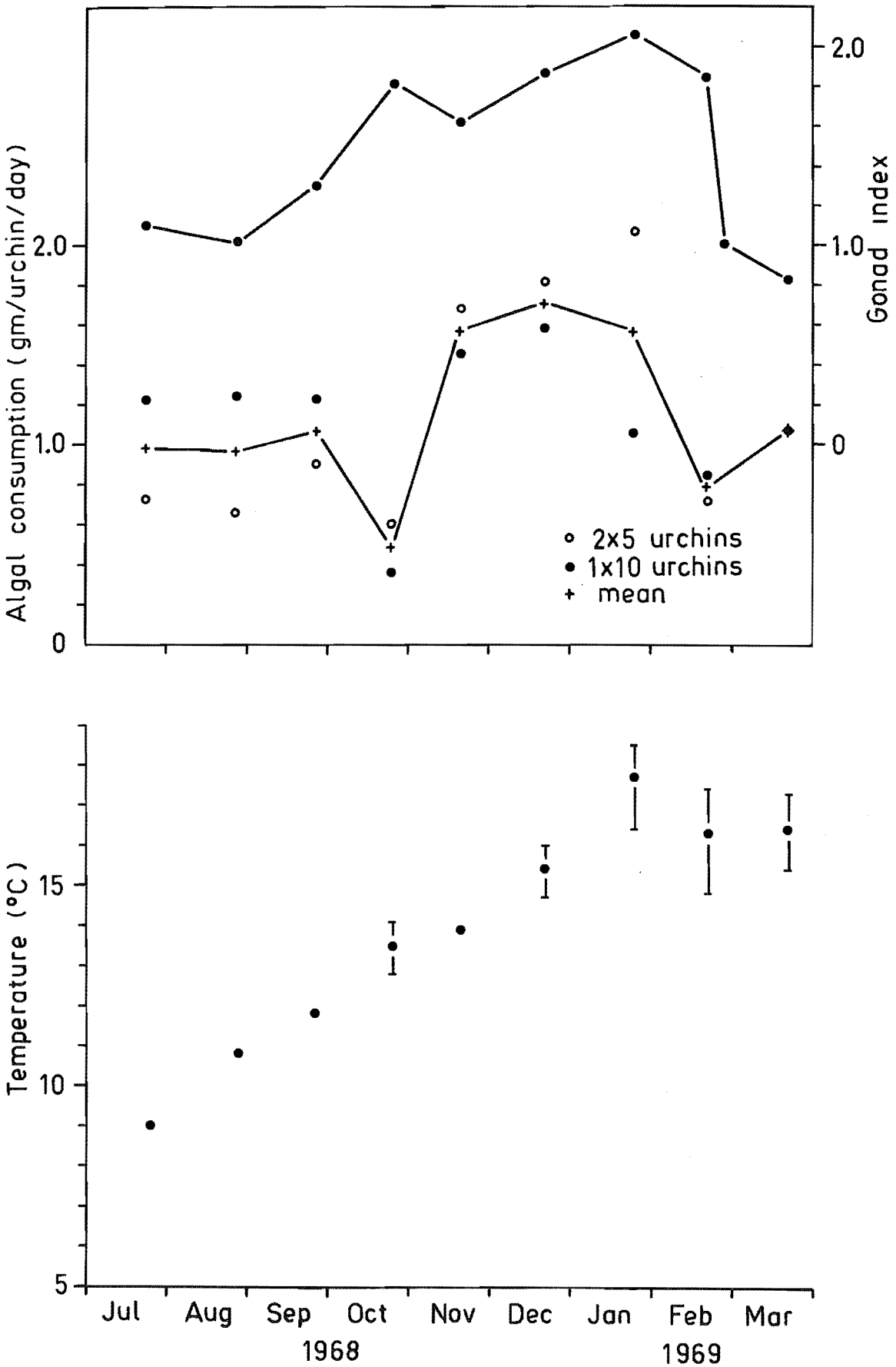

Algal consumption (gm/urchin/day)
Gonad index
2.0
1.0
0
2x5 urchins
1x10 urchins
mean
Temperature (°C)
15
10
5
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
1968
1969

Figure 31

Mean gonad indices and laboratory feeding rates for St Kilda Rocks Evechinus, 1968-69. Aquarium temperatures are also indicated. Algal weight is wet (Lessonia variegata dry weight = 0.145 wet weight in gm).

however, when the gonads are more active, food reserves in the gut walls might be utilised for gonad growth, resulting in a decrease in gut weight.

TABLE 25 : Gut indices of fed and starved Evechinus

Sample	Mean gut index		Significance of difference	
	Fed	Starved	t	P
Kaikoura	3.53	1.20	18.7	< 0.001
Kaiteriteri	4.97	1.14	16.1	< 0.001

Fuji (1962) found, however, for Strongylocentrotus intermedius that "... during the pre- and incompletion spawning period ... urchins feed only rarely, but after completion of spawning they become excessively voracious throughout the winter until the following breeding season." Decreases in feeding rate in Evechinus during the summer could explain the observed fall in gut indices since during decreased feeding food reserves might be utilised for gonad growth and other purposes.

Laboratory studies, however, did not show a summer decrease in feeding rate. Mean feeding rates for five urchins apart and then together and also mean gonad indices of the specimens and temperatures recorded during the experiments are shown in Figure 31. The rate of consumption of the brown algae Lessonia variegata tended to increase with increasing gonad index although a considerable fall in feeding rate occurred around the time of major spawn-out in February. Possibly Evechinus reduces its food consumption while spawning as was indicated for Strongylocentrotus intermedius (Fuji, 1962; Kawamura, 1964, 1965, pers. comm.). The reasons for the October decrease in feeding rate are uncertain although large amounts of silt entered the aquarium during the experiments and these may have affected feeding. No obvious relationship between feeding rate and temperature was shown by the feeding rate experiments

(Fig. 31) in contrast to the work of Moore and McPherson (1965) on the urchins Tripneustes esculentus and Lytechinus variegatus.

Thus the summer decrease in gut size observed in the Seal Reef samples may not be related to decrease in feeding rate. Utilisation of food for gonad processes may not be completely compensated for by increased food consumption, and gut reserves may be required.

The relationship between food stored in the gut and that stored and utilised in the gonad appears to be complex. Experiments more refined than those outlined would be required to clarify the whole situation.

10.5 Summary

1. Mean monthly gonad indices of Evechinus at Kaikoura and Kaiteriteri showed annual cycles, reaching peak values during the summer and decreasing to autumn minimums which were followed by increases during the winter and spring. Only one major summer peak was observed at Kaikoura but two were at Kaiteriteri. The maximum mean gonad index of Kaiteriteri specimens was just higher than the minimum for Kaikoura. Estimates of minimum annual spawn production were also much greater at Kaikoura. The lower gonad indices, absolute gonad size, and production at Kaiteriteri are attributed to the smaller amounts of food in this area. Females spawn volume was greater than that of males although the difference was not marked at Kaiteriteri.

2. Gametogenic cycles at Kaikoura and Kaiteriteri were also annual and were correlated with the gonad index cycle. A progressional development from unripe to ripe occurred during the late autumn, winter and spring. Most spent urchins were found in early autumn at both localities although 35% were spent in midsummer at Kaiteriteri. The Kaikoura pattern was similar in the two years of study.

3. Kaikoura urchins possessed ripe gametes for a greater part of the year than those at Kaiteriteri.

4. The presence of large individuals with small dark gonads at all parts of the year, particularly at Kaiteriteri,

indicates that reproductive senility may occur.

5. Male urchins possessed ripe gametes for a greater part of the year than females. They could also be induced to spawn over a longer period.

6. While major spawning occurred in late summer or early autumn at Kaikoura, some fractional spawning probably occurred throughout the summer when ripe gametes are present. Considerable spawning occurred in early as well as late summer at Kaiteriteri.

7. Kaikoura Evechinus mature at a larger size than those at Kaiteriteri, but they mature at similar ages in both localities (third and fourth years).

8. Sex ratios of mature Kaiteriteri Evechinus did not differ significantly from 1:1. Some Kaikoura populations were similar but overall, males were significantly more predominant.

9. The relative gut size at Kaikoura showed seasonal changes which were out of phase with the gonad index cycle, the gut decreasing in size as the gonad approached peak size in summer. Although Evechinus gut walls probably store food, some of which may be utilised by the gonad, decrease in gut size did not appear to result from decrease in food consumption.

11. AGE AND GROWTH

11.1 Introduction

Moore (1966, citing Fisher-Piette, 1948) suggested that "growth rate ... is perhaps the most illuminating ... parameter" used to define the well-being of an organism. Age structure is also considered as a "vital statistic" of an animal population (e.g. Ricker, 1958).

In the present study, estimation of growth rates and age structures was considered essential to gain an understanding of different population size structures and also environmental effects.

A variety of methods is available for the study of test growth rate and often age in sea urchins, most of which have been commonly used by fisheries biologists. Methods used, together with examples of workers using these for urchins, may be summarised:

(a) Analysing size frequency distributions, often with the help of probability paper ("Peterson method") (Ebert, 1968; Fuji, 1963; references in Swan, 1966);

(b) Tracing the progression of prominent modes in size frequency distributions (Ebert, 1968; Fuji, 1963; McPherson, 1965; Lewis, 1958);

(c) From mean or individual measurements of urchins,

(i) in pens or enclosures in nature (McPherson, 1965; Swan, 1960, 1961),

(ii) in aquaria (Lewis, 1966; McPherson, 1968; Moore et al., 1963a and b),

(iii) in natural areas which are considered to be isolated (Lewis, 1966; Randall, Shroeder and Stark, 1964);

(d) Mark-recapture experiments (Ebert, 1967a, 1968; Fuji, 1962, 1963; McPherson, 1965, 1968);

(e) Individual aging techniques (Moore, 1935).

Certain features of the biology of Evechinus, together with practical considerations, limited the choice of methods. None of the population size distributions could be analysed successfully with the probability paper method, and because no populations showing strong representation of young individuals were located

until late in the study, tracing of modes in size frequency distributions was impractical. Because of the wave exposed nature of the shores and shallow subtidal areas at Kaikoura, enclosure of Evechinus in pens was also impractical. Although enclosures might have been successful at Kaiteriteri, this area was only visited monthly so that supervision of the pens and provision of food would have been unsatisfactory. No enclosed intertidal pools suitable for regular examination of samples were located at Kaikoura although one was at Kaiteriteri; a group of urchins at the latter locality was examined each month from January to October 1968. Groups of urchins were maintained in running seawater aquaria from 6 to 13 months. Tagging did not yield any data on growth rate (Section 9.3).

Early in the study, a variety of techniques was investigated in an attempt to age individual Evechinus and a method was developed which gave satisfactory estimates of age in years, this providing data on both growth rate and age structure of populations.

11.2 Age Determination

11.2a Introduction

Individual age determination of organisms typically involves counting growth discontinuities (bands, lines or ridges) which occur with regular and/or known periodicity. Several workers have noted the existence of growth lines (or suspected growth lines) in or on echinoid test plates (Deutler, 1926; Moore, 1935; Zoeke, 1952; Durham, 1955; Gamble, 1967; Larsson, 1968) and spines (Swan, 1952; McRae, 1959; Moore, 1966; Ebert, 1967b and references in latter). These workers were all interested in the possibility of using the growth lines as age indicators but few made systematic investigations into their correlation with age. Moore (1935) clearly demonstrated that growth lines in the apical plates of Echinus esculentus were annual. Although G. P. Moore (1966) for Heliocidaris erythrogramma and Ebert (1967b) for Strongylocentrotus purpuratus found that the number of cycles of trabecular bands in

the spines was positively correlated with test size, Ebert suggested that the cycles were not annual but were a result of breakage and regeneration.

The present investigation was concerned with the search for and then successful demonstration of growth lines and testing their correlation with age. The investigation was also concerned with consideration of the skeletal elements most suitable for age determination.

11.2b Methods

The spines, elements of Aristotle's lantern and test plates of Evechinus were examined using a variety of techniques to find and then efficiently demonstrate growth lines. But for reasons discussed below most effort was expended in examination of horizontally sectioned and chemically treated apical plates.

Both thin sectioned and polished plates, prepared by the Geology Department, University of Canterbury, did not show growth lines clearly. Unmounted, sectioned plates were then etched in weak organic (acetic, formic, lactic) and inorganic (HCl) acids and as a further refinement the cellulose peel technique outlined by Ager (1965) was tried. Treatment of plates with a weak solution of sodium hypochlorite (see Durham, 1955) was tried unsuccessfully. While etching vaguely showed growth lines which appeared faintly on cellulose peels it seemed that the lines contained pigment so that histological methods involving staining and/or clearing were attempted.

Clearing in xylol using the methods of Moore (1935) did not give satisfactory results but plates cleared in glycerine (sometimes used in examining fish otoliths; Mundy, 1968) showed more promise. Rotonene which has been successfully used for staining fish otoliths (Mundy, 1968) did not selectively stain any parts of sectioned plates; neither did thionin (used for demonstrating growth lines in mammalian teeth; I. Stirling, pers. comm.).

Since lactic acid as an etching agent, and glycerine as a clearant, helped show growth lines independently, they were then

tried together with phenol as lactophenol. This gave better results than any of the above methods. Lillie's (1957) observations that melanins selectively uptake ferrous ions then prompted me to add these to the lactophenol as ferrous sulphate. This caused pronounced darkening of the growth lines. Thus, the following method, combining etching, clearing and staining, was evolved for efficiently demonstrating growth lines.

A portion of the test including the apical plates was removed from the urchin with a hacksaw and then dried in air for several days. After this, a horizontal section of all the apical plates was prepared by sectioning on a disc grinder supplied with a steady stream of water. The ground plates were then immersed in lactophenol containing ca 0.5% ferrous sulphate for a few minutes and then examined under a dissecting microscope.

As no known age Evechinus were available, indirect checks on the validity of age determinations were used. To find when and how often growth bands were formed, seasonal changes in the edges of apical plates, prepared as above, were noted for at least 50 urchins per month at both Kaikoura and Kaiteriteri, for one year at each locality. Edges were classified as narrow light, medium light, wide light, narrow dark, medium dark or wide dark and the percentage of urchins showing each category was noted each month.

Mundy (1968), for the sandflounder Rhombosolea plebia, indicated that if an otolith is to be a satisfactory age indicator, a basic relationship between otolith size and fish length must exist. The same should apply to the plates used as age indicators in Evechinus and urchin diameter. Accordingly, for 44 specimens from St Kilda Rocks, February 1969, the relationship between apical plate width and test diameter was investigated for all apical plates (genitals, insert and exsert oculars, and madreporite - although the latter was not used in age determinations).

The growth rate of specimens estimated by aging was compared with that of a sample, placed and measured in an enclosed pool, each month at Kaiteriteri. Similarly estimated growth rates were compared for consistency for two samples taken from the same area

in September and November 1967. Mean diameters of individuals in certain year classes were also compared with sizes visually estimated from three diameter frequency distributions.

When it was suspected or found that valid data could be gained from individually aged Evechinus, samples of 200 (September 1967) and 204 (November 1967) from Kaiteriteri and 150 (July 1967), 116 (March 1968) and 175 (July 1968) from Kaikoura were examined for age.

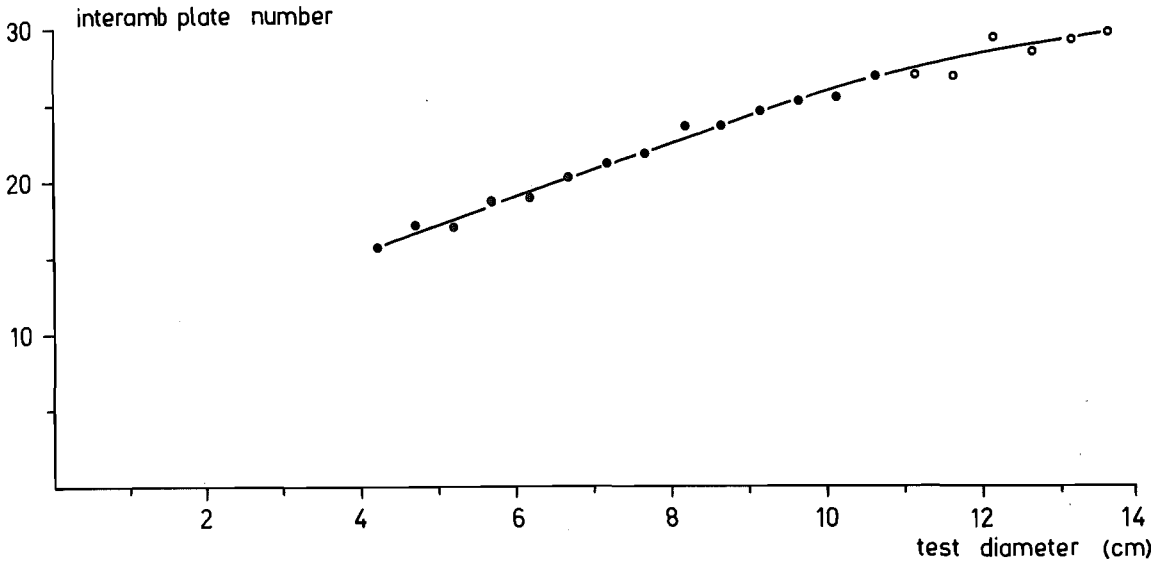
11.2c Results and discussion

i. Growth bands

Cycles of trabecular bands were readily seen in mounted, longitudinally sectioned spines (see also McRae, 1959). But since spines are readily lost and since replacement spines may not have the same number of trabecular bands as originals (Swan, 1952, 1966) it was decided not to pursue their possible use as age indicators. This seems fortunate since Ebert (1967b) has suggested that the trabecular bands of Strongylocentrotus purpuratus are not annual but are related to spine breakage and regeneration.

Although relatively little effort was expended, growth lines were not found in any of the elements of Aristotle's lantern.

Growth lines were readily demonstrated, using the methods above, in the coronal and apical test plates. While Moore (1935) used genital plates for age determination he stated that any plates could be used; similarly Durham (1955) and Gamble (1967) suggested that coronal plates could be used. It has been found, however, that urchin test growth takes place not only by the growth of formed coronal plates but also by the addition of new plates (Cutress, 1965; Hsai, 1948; Swan, 1966). This is also true of Evechinus. The number of interambulacral plates in one column was counted and expressed as a mean for each 5mm diameter class in samples of 48 from Seal Reef and 150 from Wakatu Point, Kaikoura. Figure 32 shows a steady increase in the number of interambulacral plates per column with increase in test diameter. Thus the coronal plates


interamb plate number
30
20
10
2
4
6
8
10
12
14
test diameter (cm)

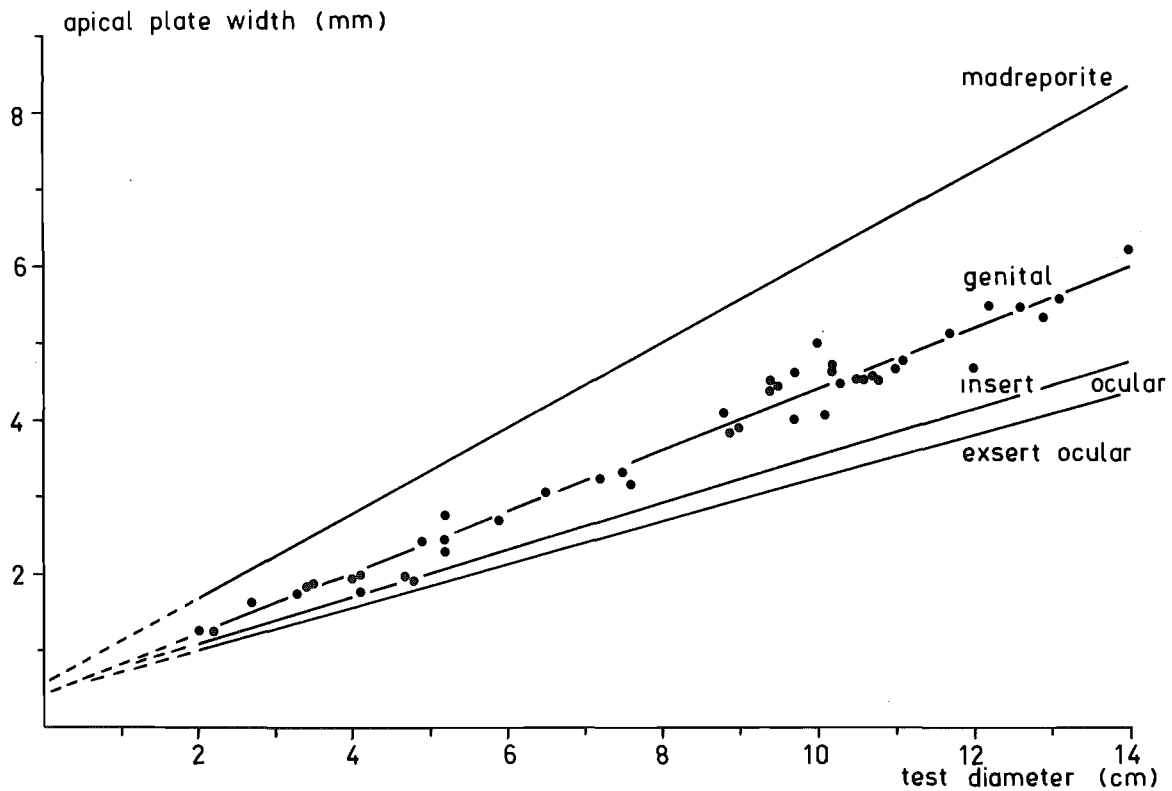
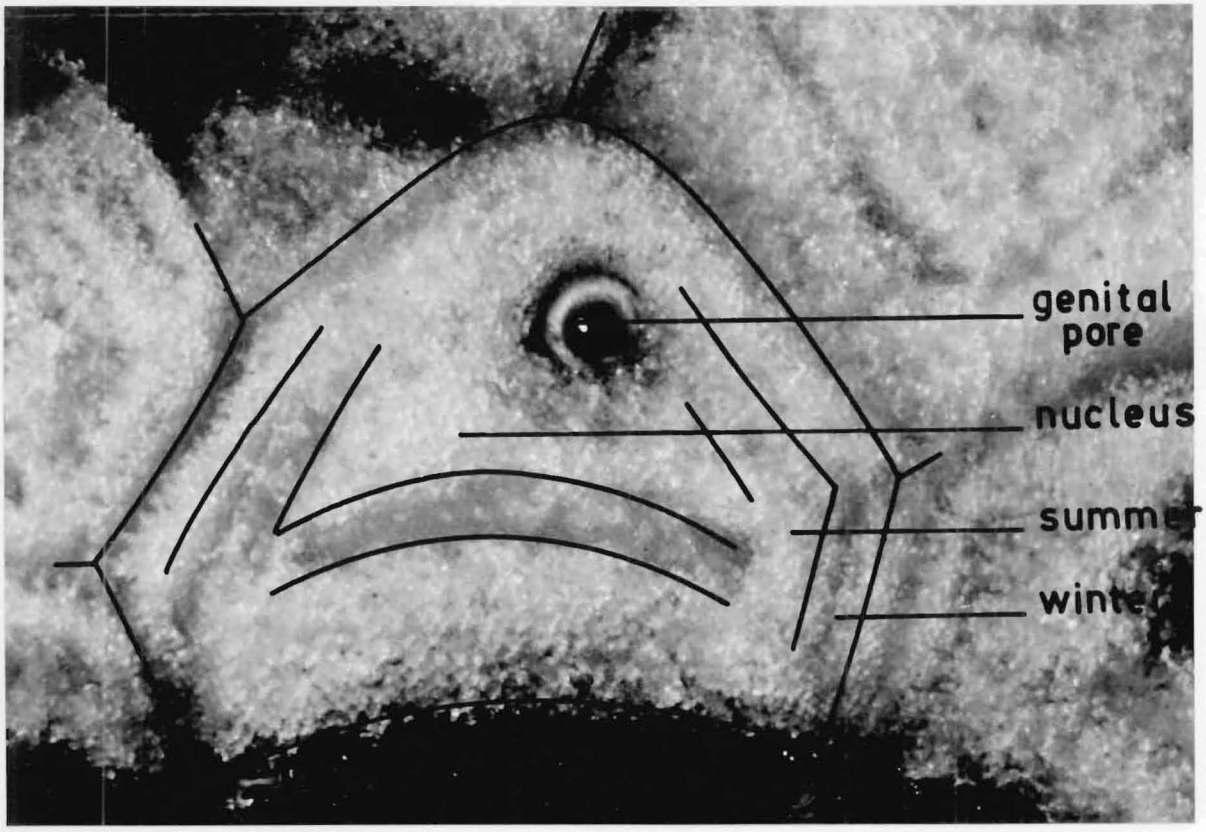

apical plate width (mm)
8
6
4
2
madreporite
genital
insert ocular
exsert ocular
2
4
6
8
10
12
14
test diameter (cm)

Figure 32

Number of interambulacral plates per column with respect to test diameter in Wakatu Point and Seal Reef Evechinus.

Figure 33

Apical plate widths with respect to test diameter in St Kilda Rocks Evechinus. Points are plotted only for the madreporite width; others showed similar scatter and all regressions were significant to less than the 0.001% level.


genital pore
nucleus
summer
winter

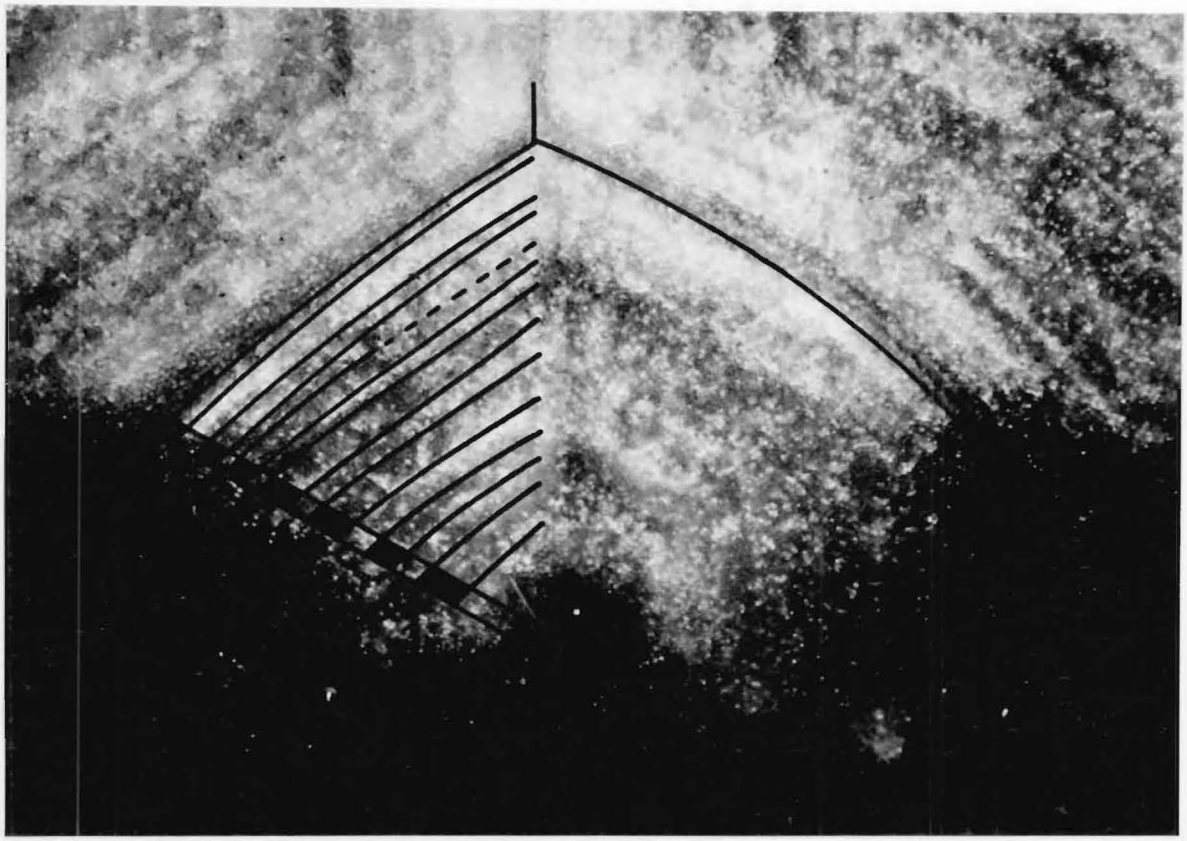


Plate 7

Horizontal section of a treated genital plate from a 2.6cm diameter St Kilda Rocks Evechinus, showing light nucleus, one summer and one winter growth band. Plate width 1.5mm. Photo, B. M. Dukes.

Plate 8

Horizontal section of a treated ocular plate from a 10.1cm diameter St Kilda Rocks Evechinus, showing six complete and one incomplete summer growth bands. Plate width 3.2mm. Photo, B. M. Dukes.

are not all of the same age. In fact, the only known age test plates are those of the apical system, for these are formed at metamorphosis (Gordon, 1926, 1929) and remain for the rest of the urchin's life. It is these plates which must be used in age determinations.

Growth lines could generally be counted on at least one of the nine genital or ocular plates and often readings on one could be checked with those on others; but reliable counts could not be made on all individuals (Figs. 39 - 42).

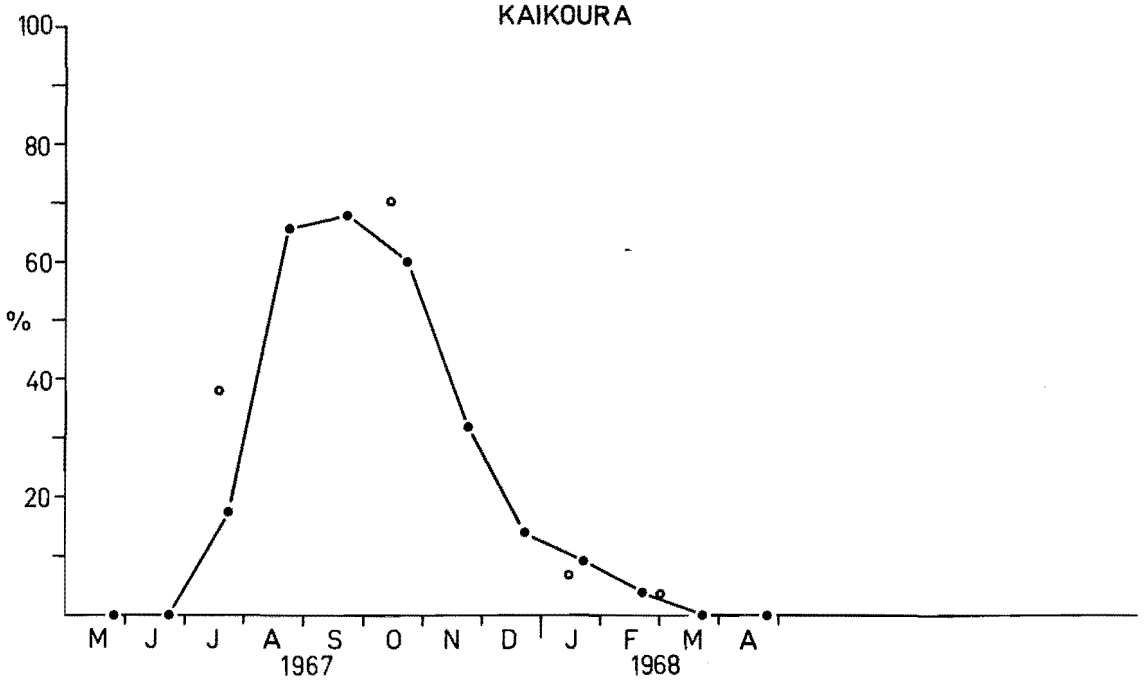
Photographing growth lines proved extremely difficult. Several factors brought this about. Firstly, the growth lines showed best for only a brief period after immersion in the lactophenol solution; after further exposure to air the plates darkened. To postpone darkening the plates were immersed in glycerine. Secondly at the time when growth lines showed best, the solution was still active in the plates forming effervescing bubbles. While these could be repeatedly brushed away during routine examinations, they proved an obstacle to photography; neutralising the acid was of little help. Finally, the porous and rough nature of the plate surfaces resulted in "highlighting" effects when they were illuminated for photography.

Photographs of growth lines together with overlay interpretations are, however, given for apical plates from two Evechinus (Plates 7 and 8). They show one dark (summer) band, and six complete and one incomplete dark bands. It may be noted that each band is typically darker at its edges than in its centre. If the plates were treated too long in the lactophenol solution the dark bands sometimes appeared double. But experience in reading generally removed the confusion possible from this.

ii. Validation of aging techniques

Seasonal changes in the frequency of a wide light band on the outside edges of apical plates for Kaikoura and Kaiteriteri samples are shown in Figure 34. Only one peak was found over a year's sampling, this being formed mainly during the winter. Other outside edge categories also showed single peaks (Table 26), wide dark

KAIKOURA



KAITERITERI

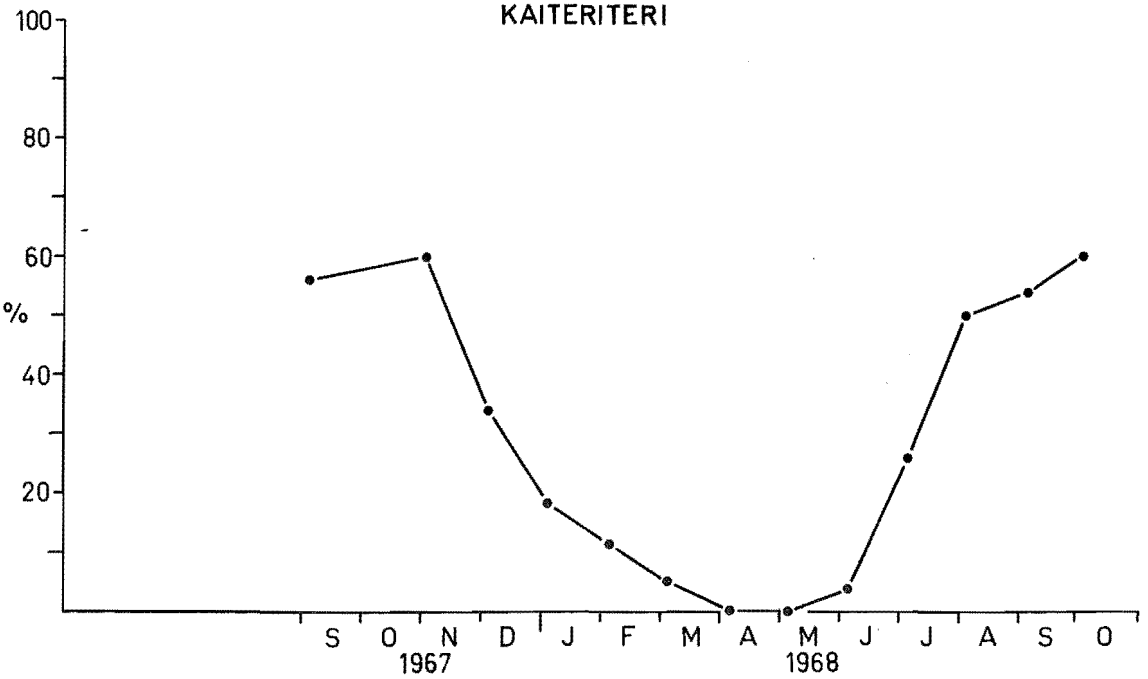


Figure 34

Seasonal changes in the frequency of wide light bands in the apical plates of Kaikoura and Kaiteriteri Evechinus. Open circles are additional samples from Wakatu Point and Waeroa Point.

TABLE 26 : Percentages of Evechinus showing the different outside edges of apical plates, at Kaikoura and Kaiteriteri.

KAIKOURA	Outside edge					
Date	Narrow dark	Medium dark	Wide dark	Narrow light	Medium light	Wide light
25. 5.67	0	0	0	95.8	4.2	0
23. 6.67	0	0	0	86.0	14.0	0
24. 7.67	0	0	0	25.0	58.3	16.7
28. 8.67	0	0	0	8.0	24.0	68.0
22. 9.67	28.0	0	0	0	4.0	68.0
23.10.67	42.0	4.0	0	0	4.0	50.0
24.11.67	52.0	16.0	0	0	0	32.0
26.12.67	54.0	30.0	2.0	0	0	14.0
24. 1.68	38.0	32.0	6.0	0	0	14.0
23. 2.68	22.0	42.0	32.0	0	0	4.0
22. 3.68	14.0	28.0	48.0	10.0	0	0
24. 4.68	0	12.0	34.0	46.0	8.0	0
KAITERITERI						
7. 9.67*	4.3	1.4	0	7.9	40.0	46.4
8. 9.67**	1.5	0	0	3.0	40.0	55.5
4.11.67	27.9	4.7	0	0	6.9	60.5
3.12.67	56.0	8.0	0	0	2.0	34.0
3. 1.68	50.0	30.0	2.0	0	0	18.0
2. 2.68	40.0	36.0	12.0	0	0	12.0
4. 3.68	16.0	50.0	28.0	0	0	6.0
8. 4.68	8.0	26.0	56.0	10.0	0	0
7. 5.68	2.0	10.0	36.0	48.0	4.0	0
9. 6.68	0	2.0	14.0	56.0	26.0	2.0
8. 7.68	0	0	2.0	24.0	52.0	26.0
6. 8.68	2.0	0	0	6.0	32.0	60.0
6. 9.68	10.0	0	0	2.0	27.0	54.0
7.10.68	38.0	0	0	0	2.0	60.0

* sample of 140; ** sample of 200; all other samples 50

bands occurring mainly in late summer. Thus only a single dark and a single light band was formed each year, at least in the samples studied. The seasons of formation were similar to those of Echinus esculentus (Moore, 1935).

The relationships between apical plate widths and test diameter were markedly linear (Fig. 33) all least square linear regression coefficients being highly significant (Table 27).

TABLE 27 : Least square regressions of mean apical plate widths (w, in mm) on test diameter (d, in cm) for 44 urchins from St Kilda Rocks.

Plates	Regression equation	Significance of regression coefficient	
		t	P
Genital (4)	$w_g = 0.397d + 0.405$	39.700	< 0.001
Insert ocular (2-3)	$w_i = 0.301d + 0.498$	33.444	< 0.001
Exsert ocular (3-2)	$w_e = 0.277d + 0.449$	30.778	< 0.001
Madreporite* (1)	$w_m = 0.551d + 0.591$	30.661	< 0.001

* not used for age reading

The mean diameters of specimens placed in the pool at Kaiteriteri, between January and July 1968, are shown in Figure 37. In the three months after this, numbers were so reduced that mean sizes were not then considered reliable indicators of growth. Growth during the first six months (which included late summer, autumn, early and midwinter) was ca 5.0mm in diameter. Assuming that growth rates did not differ markedly during the spring and early summer (Section 11.3b), an annual growth rate of about 1.0cm is indicated. That predicted from individually aged urchins from the same area was also ca 1.0cm (Section 11.3a).

Mean diameters of year classes calculated from two individually aged samples at Kaiteriteri (September and November 1967) were compared by t-tests (Table 28).

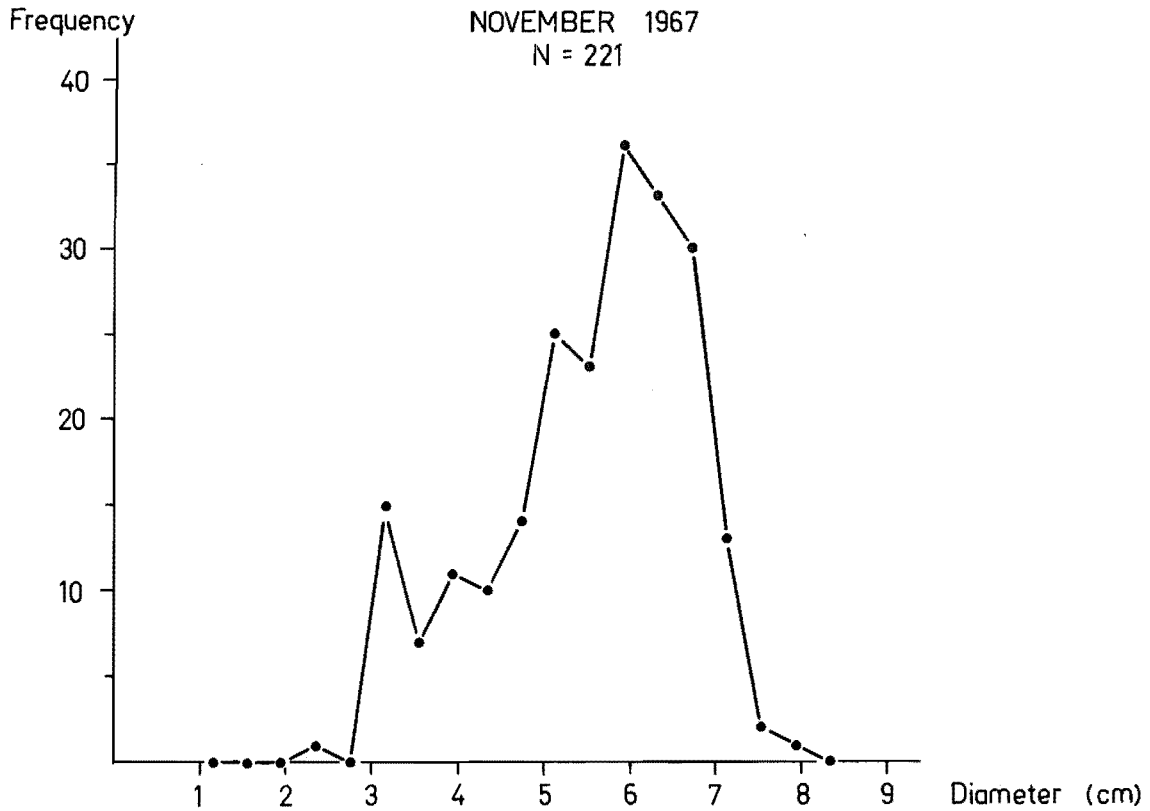
TABLE 28 : Mean diameter ($\bar{d}$) of individually aged Evechinus at Kaiteriteri, September and November 1967.

Year class		2+	3+	4+	5+
8 September	N	29	16	45	67
	$\bar{d}$	2.94	4.10	5.05	5.93
8 November	N	52	46	37	20
	$\bar{d}$	3.13	4.12	5.01	5.80
	t	1.92	0.15	0.39	1.46
	P	$0.1 > P > 0.05$	$0.9 > P > 0.8$	$P \div 0.7$	$0.2 > P > 0.1$

The mean size of 2+ years specimens was 0.19cm greater in November, a barely significant difference, while none of the other mean sizes differed significantly. If growth were greater than 1.0cm per year (0.08cm per month assuming no seasonal variation) greater differences between the September and November means would have been expected.

The Wakatu Point (July 1967) and Waeroa Point (March 1968) samples show a general agreement between smaller diameter peaks in their diameter frequency distributions and year classes, particularly 2+ and 3+ years Wakatu Point urchins and 2 year Waeroa Point specimens (Figs. 39 and 42).

A subtidal population at Kaiteriteri showed marked differences between the diameter frequency distributions of November 1967 and November 1968 (Fig. 35). A strong mode at ca 2.0cm, present in 1968, was not present in 1967 and the mode at just over 3.0cm in 1967 was not represented in 1968. These suggest that a year class was absent from the population. Age readings in November 1967 showed only one 1+ years specimen but a further analysis in 1968


Frequency
NOVEMBER 1967
N = 221
40
30
20
10
1
2
3
4
5
6
7
8
9
Diameter (cm)

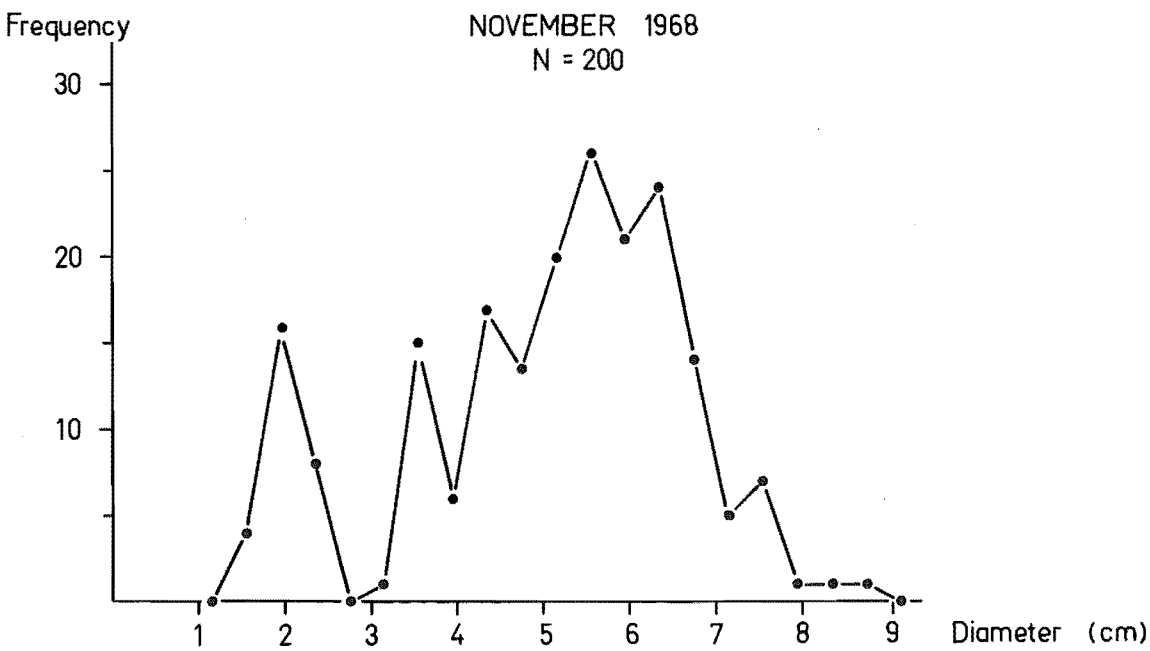

Frequency
NOVEMBER 1968
N = 200
30
20
10
1
2
3
4
5
6
7
8
9
Diameter (cm)

Figure 35

Diameter frequency distributions of a subtidal Kaiteriteri population, November 1967 and 1968.

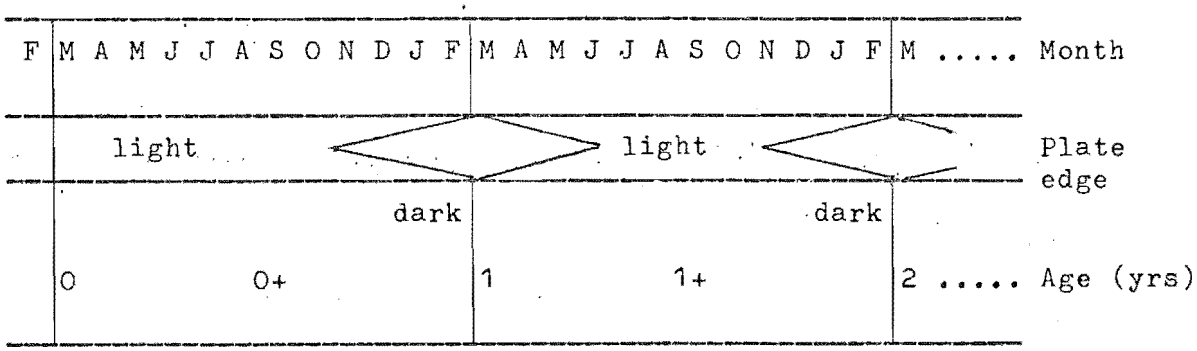
showed that all urchins in the 2.0cm mode were 1+ years old; no 2+ years urchins were found at this time (0+ years urchins, which were probably only 5mm diameter, were overlooked in the samples). The diameter separation between the first mode in 1968 and the gap in 1968 and also the first mode in 1967 is ca 1.0cm (Fig. 35). This is the same as the annual growth rate predicted from age readings (Section 11.3a).

11.2d Conclusions

The above indicates that growth bands can be demonstrated in the test plates and that age estimates using the growth bands of apical plates are acceptable. But in all samples, some individuals could not be aged with certainty.

The actual age of an Evechinus, as related to the number of growth bands, may now be explained. Evechinus breeds mainly in late summer (Section 10.3a) and larval life span probably averages one month (Section 9.2). Therefore the time of settling and metamorphosis (assigned age 0) may be taken as approximately March or early April. During the autumn, winter and early spring a light nucleus is formed (Fig. 34); over this period urchins are age 0+ years. The light band is followed by a dark band, formed mainly during the summer; animals reach age 1 after the end of summer. The relationship between growth bands and age is summarised in Table 29.

TABLE 29 : Relationship between growth bands and age in Evechinus



Thus, the animal shown in Plate 7 is 1+ years old and shows a winter nucleus, a summer dark band and a winter outside edge. Plate 8 is from an urchin nearly 7 years old; six complete dark bands and one incomplete dark edge are present.

11.3 Growth rate

11.3a Results

Growth rate curves derived from individually aged Evechinus at Kaikoura (Wakatu Point and St Kilda Rocks) and Kaiteriteri are shown in Figure 36. Parts of the samples were not aged or could not be aged with certainty (Figs. 39, 40 and 41) but there is no reason to suspect that this significantly biased the results.

All growth curves show the usual pattern of linear growth, the growth rate slowing with increasing age.

Growth rates at both Kaikoura localities were greater than at Kaiteriteri and growth continued to a greater age at St Kilda Rocks (depth 8 - 12m) than at Wakatu Point (depth 1 - 3m). As found for Strongylocentrotus purpuratus (Ebert, 1968) the different growth rates of Evechinus were reflected in the size of the animals. The largest Kaiteriteri urchin found had a test diameter of 9.7cm and few were greater than 8.0cm while the largest St Kilda Rocks specimen measured 15.2cm diameter, and fair numbers were more than 14.0cm. The largest Wakatu Point specimen was 10.9cm diameter. The largest known Evechinus recorded by Mortensen (1943) was 14.5cm in diameter; the 15.2cm St Kilda Rocks specimen is the largest recorded Evechinus.

11.3b Discussion

Growth rate differences have also been noted between populations of the urchins Strongylocentrotus purpuratus (Ebert, 1968), Eucidaris tribuloides (McPherson, 1968), Echinus esculentus (Moore, 1935), Tripneustes esculentus (Lewis, 1958; Moore et al., 1963b, summarised by Swan, 1966) and S. droebachiensis (Swan, 1961). Ebert (1968) indicated that growth rates in S. purpuratus were

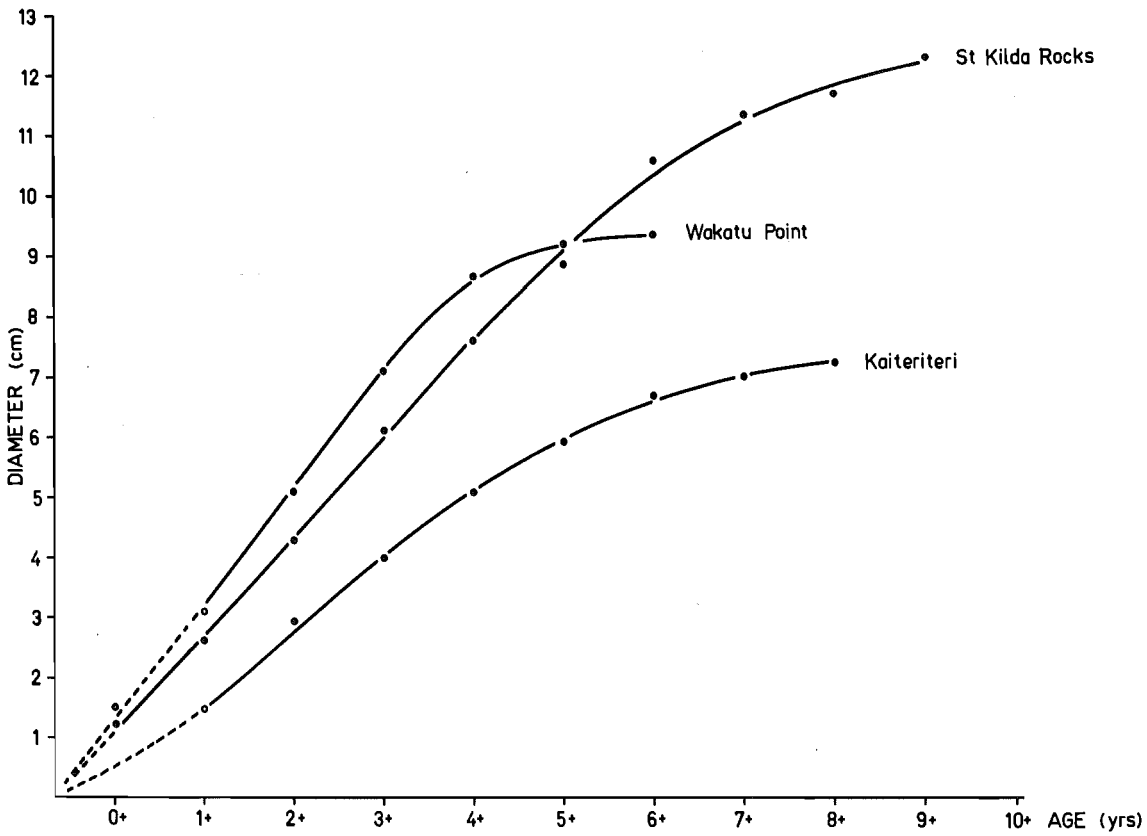

DIAMETER (cm)
13
12
11
10
9
8
7
6
5
4
3
2
1
0+
1+
2+
3+
4+
5+
6+
7+
8+
9+
10+
AGE (yrs)
St Kilda Rocks
Wakatu Point
Kaiteriteri

Figure 36

Annual growth rate of Evechinus at St Kilda Rocks and Wakatu Point, Kaikoura, and Kaiteritəri. Open circles were suggested from a size frequency distribution (Wakatu Point) and other aged samples (Kaiteriteri).

limited by food availability, the effects of which were modified by wave action (which caused spine breakage). Moore (1935, 1966) and Swan (1961) suggested that the growth rates of E. esculentus and S. droebachiensis were related to food availability. Swan also showed that the growth rate of urchins fed on Laminaria exceeded that of those fed on Ascophyllum by more than 70%. In contrast to Moore et al. (1963b), McPherson (1968) found no correlation between differences in growth rate and temperature, but found greater growth in more sheltered areas. He did not investigate the effects of food but suggested that wave action might affect either the food available or the time available for feeding.

Temperatures are typically higher at Kaiteriteri than Kaikoura (Fig. 2) but this is unlikely to be the primary cause of the differences in growth rate since Evechinus larger than those at Kaiteriteri are found in warmer waters in the north of New Zealand.

Since Kaiteriteri was markedly more barren than Kaikoura (Section 1) it seemed probable that the lower growth rates at Kaiteriteri resulted from less available food. To test this hypothesis, groups of 20 urchins from Kaiteriteri and 18 from Kaikoura were fed or partially starved in running seawater aquaria at Kaikoura for six months (see Section 10.3d). Mean initial and final weights and test diameters are shown in Table 30 together with tests of significance of the differences.

Since none of the results in Table 30 are statistically significant, the effects of food availability on Evechinus growth remain partially unresolved. But small increases in the weight and diameter of fed specimens from both localities occurred. In contrast, small decreases in diameter occurred in starved specimens. Kaikoura starved specimens decreased slightly in weight although those from Kaiteriteri showed a slight increase, presumably due to food derived from detritus and microscopic growth in the aquarium.

Several workers have found differences between laboratory and natural growth rates in echinoids but at present there is no overall relationship between the two. Markedly reduced laboratory growth has been recorded for Lytechinus variegatus (Moore et al., 1963a)

and Tripneustes esculentus (Moore et al., 1963b) but faster laboratory growth rates have been reported for Diadema antillarum (Lewis, 1966) and Eucidaris tribuloides (McPherson, 1968).

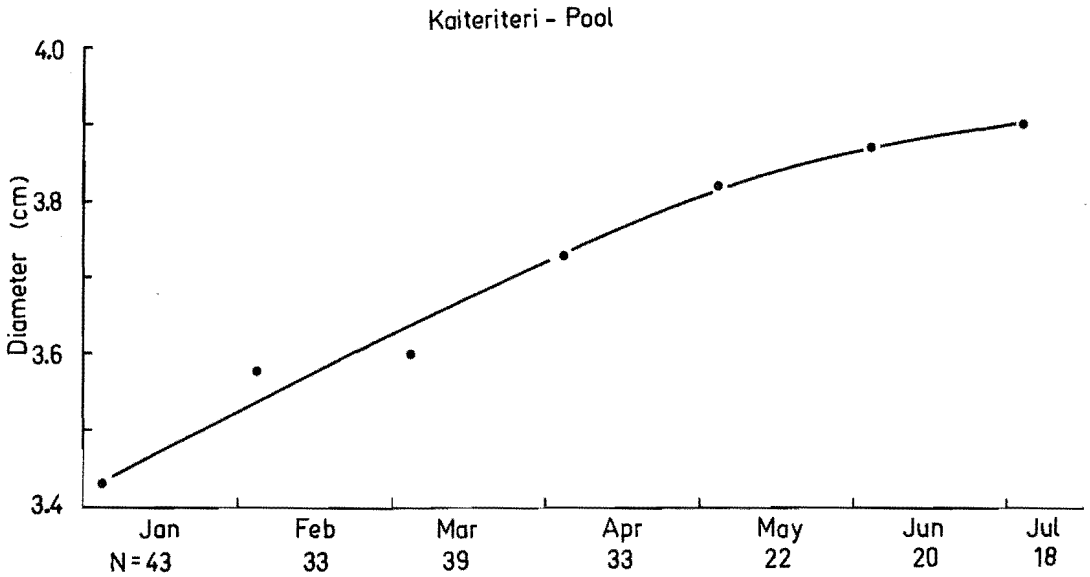
TABLE 30 : Comparison of mean sizes of fed and partially starved Evechinus, initially and after six months.

	Test diameter (cm)			Test of significance	
	Initial	Final	Change	t	P
Kaikoura Fed	3.37	3.40	+0.03	0.31	0.40 > P > 0.35
Kaikoura Starved	3.39	3.30	-0.09	0.93	0.20 > P > 0.15
Kaiteriteri Fed	3.41	3.48	+0.07	0.80	0.25 > P > 0.20
Kaiteriteri Starved	3.41	3.38	-0.03	0.31	0.40 > P > 0.35

	Weight (gm)			Test of significance	
	Initial	Final	Change	t	P
Kaikoura Fed	20.68	23.65	+2.97	1.52	0.10 > P > 0.05
Kaikoura Starved	20.66	19.22	-1.44	0.87	0.20 > P > 0.15
Kaiteriteri Fed	21.24	23.96	+2.72	1.60	0.10 > P > 0.05
Kaiteriteri Starved	20.87	21.30	+0.43	0.25	0.45 > P > 0.40

Conditions provided in the laboratory at Kaikoura appeared to be unsuitable for normal Evechinus growth to occur (see Table 30). This is also evident from the growth of small Kaikoura specimens in an aquarium (Fig. 38). These showed a mean annual increase in diameter of 0.9cm, while natural populations at Kaikoura would have increased about 1.5cm (Fig. 36).

Little can be said regarding the differences in growth observed at St Kilda Rocks and Wakatu Point. These localities are separated by less than 1 km but variations in the growth of


Kaiteriteri - Pool
4.0
3.8
3.6
3.4
Diameter (cm)
Jan
N = 43
Feb
33
Mar
39
Apr
33
May
22
Jun
20
Jul
18

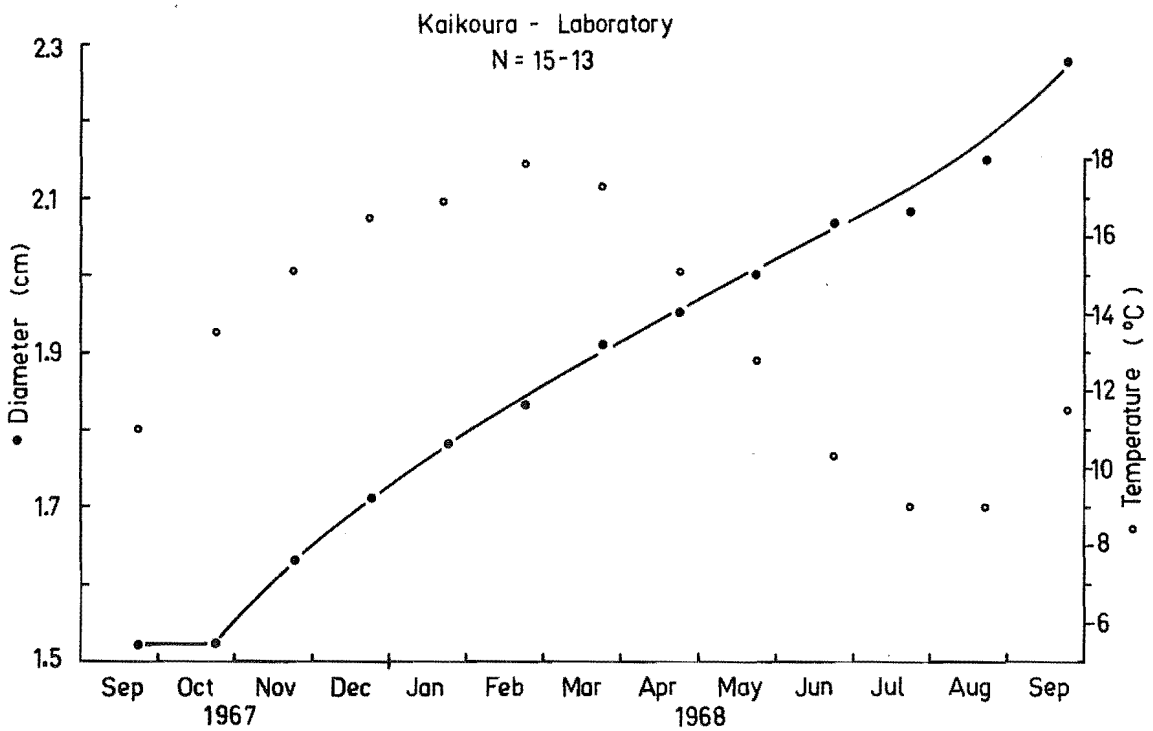

Kaikoura - Laboratory
N = 15-13
2.3
2.1
1.9
1.7
1.5
• Diameter (cm)
18
16
14
12
10
8
6
° Temperature (°C)
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
1967
1968

Figure 37

Mean growth rate of Evechinus placed in a pool at Kaiteriteri, January to July 1968. Previous to this experiment 73 urchins were removed from the pool.

Figure 38

Mean growth rate of Evechinus in a running seawater aquarium at Kaikoura, September 1967 to 1968. Aquarium temperatures are also shown.

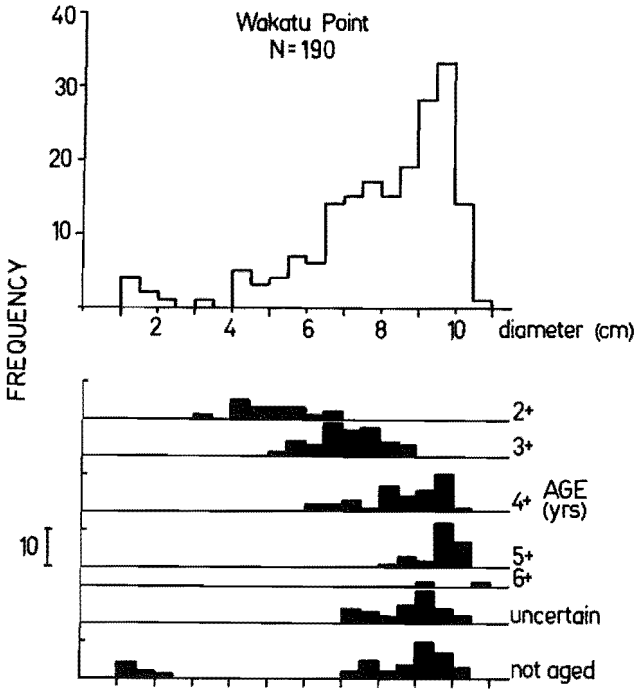
populations separated by only 20 to 30m have been recorded for Strongylocentrotus purpuratus (Ebert, 1965b, 1968). The two Kaikoura localities differ in at least depth and wave exposure (Section 3.2), but environmental effects were not specifically investigated in a manner similar to that of Ebert (1968).

Little data on seasonal patterns of test growth were obtained. Juvenile specimens kept in the aquarium at Kaikoura, however, did not show marked seasonal changes in growth rate (Fig. 38) despite the fact that temperatures varied from 9.0 to 17.9°C. Over the six months of study, little change in the growth rate of specimens in the pool at Kaiteriteri occurred (Fig. 37). Little significance is attached to the slower growth in May, June and July since reduction in sample size may have biased the results.

The possibility of seasonal changes in growth rate cannot, however, be discounted. Seasonal variations have been recorded in the growth rates of the urchins Echinus esculentus (Moore, 1935), Tripneustes esculentus (Moore et al., 1963b), Eucidaris tribuloides (McPherson, 1968) and Strongylocentrotus purpuratus (Ebert, 1968). That the dark growth bands in the apical plates of larger Evechinus are typically narrower than the light bands, despite the fact that they take similar times to form, may indicate reduced summer growth. But seasonal changes in growth rate may be less in small Evechinus as indicated from their laboratory growth (Fig. 38) and also since dark bands in their apical plates were relatively wider than in larger urchins. Moore et al. (1963b) found little seasonal variation in the growth rate of small Tripneustes esculentus.

11.4 Age Structure

Comparison of Evechinus population age structures at Kaikoura and Kaiteriteri (Figs. 39, 40, 41 and 42; Table 31) suggests firstly that all populations show different age structures, year classes being represented to different degrees. Secondly, longevities differed among populations. Kaikoura urchins typically lived longer than those at Kaiteriteri and the deeper subtidal St Kilda Rocks population showed greater longevities than shallower subtidal


Wakatu Point
N=190
FREQUENCY
40
30
20
10
2
4
6
8
10
diameter (cm)
2+
3+
4+
AGE
(yrs)
5+
6+
uncertain
not aged
10

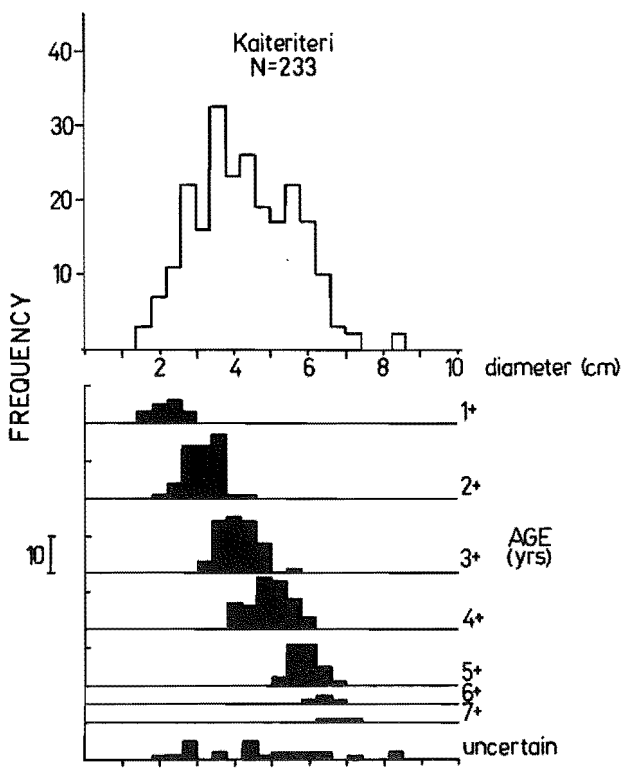

Kaiteriteri
N=233
FREQUENCY
40
30
20
10
2
4
6
8
10
diameter (cm)
1+
2+
3+
AGE
(yrs)
4+
5+
6+
7+
uncertain
10

Figure 39

Age structure of a subtidal population of Evechinus at Wakatu Point, July 1967.

Figure 40

Age structure of an intertidal population of Evechinus at Kaiteriteri, November 1967.

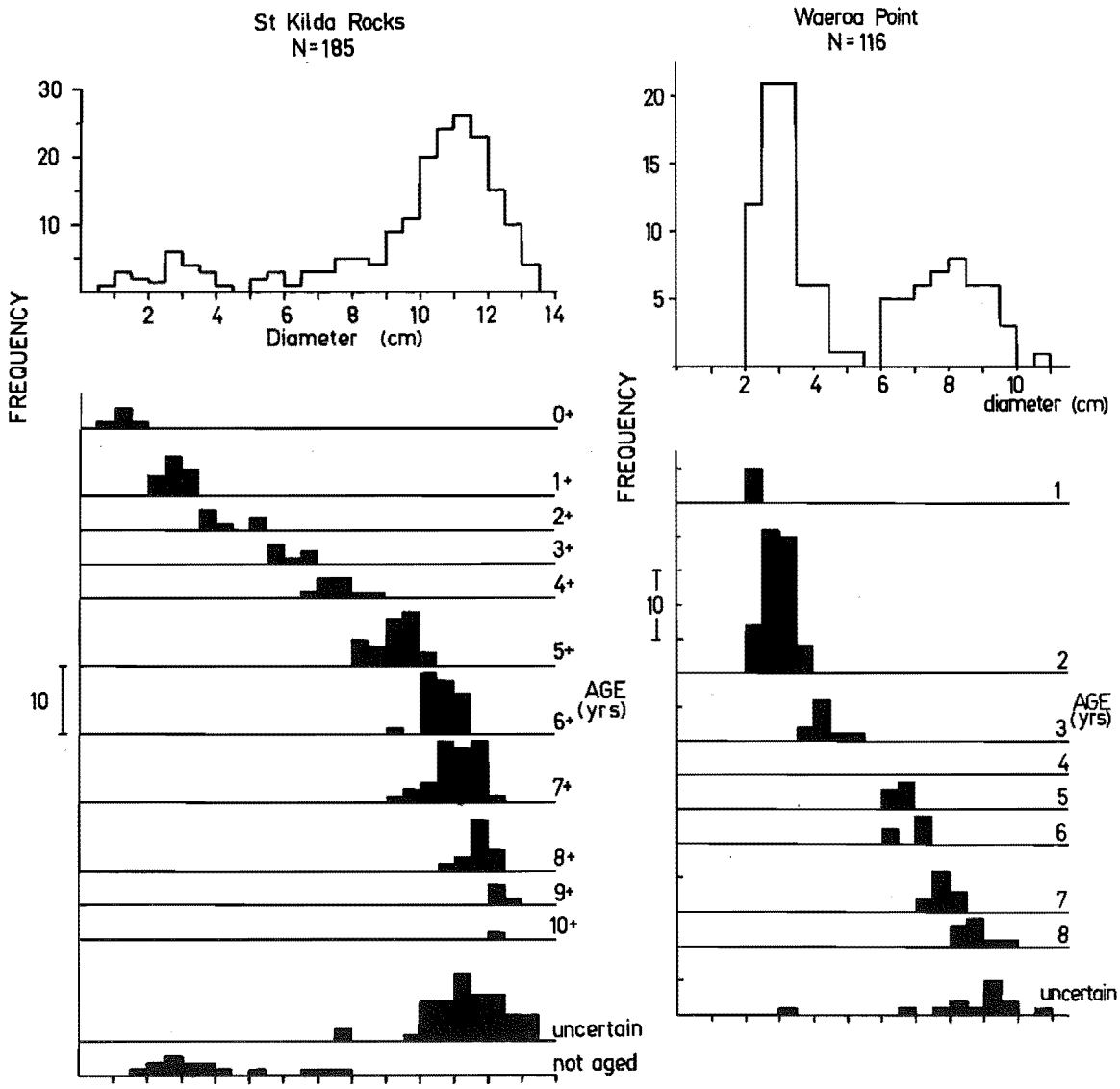

St Kilda Rocks
N=185
30
20
10
2
4
6
8
10
12
14
Diameter (cm)
FREQUENCY
0+
1+
2+
3+
4+
5+
6+
7+
8+
9+
10+
uncertain
not aged
10
AGE (yrs)
Waeroa Point
N=116
20
15
10
5
2
4
6
8
10
diameter (cm)
FREQUENCY
1
2
3
4
5
6
7
8
uncertain
10
AGE (yrs)

Figure 41 (left)

Age structure of a subtidal population of Evechinus at St Kilda Rocks, July 1968.

Figure 42 (right)

Age structure of an intertidal population of Evechinus at Waeroa Point, March 1968. Note the absence of four year specimens.

(Wakatu Point) and intertidal (Waeroa Point) Kaikoura populations. Thirdly, there was no overall trend for numbers to decrease with increasing age.

TABLE 31 : Age structures of Evechinus populations

	Aged urchins											% aged*
	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+	10+	
Kaiteriteri 3.11.67	0	15	52	46	37	20	4	4				76.4
Wakatu Point 15. 7.67	7?	1?	18	39	36	25	1					76.2
Waeroa Point 1. 3.68		10	25	10	0	5	5	10	5			70.2
St Kilda 30. 7.68	4	14	6	6	9	24	22	32	13	3	1	73.0

* this is of those investigated for age; parts of some samples were not (Figs. 39 and 41).

Except for some records of populations which showed strong representation of young age classes (e.g. McPherson, 1965; Moore et al., 1963a) and some size frequency analyses (see Swan, 1966 and Ebert, 1968) few data are available on the age structure of echinoid populations. Those of Evechinus populations will be discussed, with particular reference to the first and third points above, in Section 12.

Estimates of longevity in urchins may be summarised: two or three years for Lytechinus variegatus and Tripneustes esculentus (Moore, 1966; Moore et al., 1963a and b); at least four to five years for Eucidaris tribuloides (McPherson, 1968); four to eight years and perhaps more for Echinus esculentus (Moore, 1935); and at least ten years for Strongylocentrotus purpuratus (Ebert, 1967a) and Echinocardium cordatum (Buchanan, 1966). The present study indicates that, in some localities, Evechinus may also live at least ten years. From the growth curve at St Kilda Rocks (Fig. 36),

specimens larger than about 13.5cm could be considerably older; perhaps more than 15 years. Moore (1966) concluded that there was "clearly little general trend of longevity with temperature" but consideration of later records suggests that the longevity of tropical species may be less than that of temperate species. More data, however, are needed to substantiate this.

Test growth and gonad growth, regarded as indices of "well-being" (Moore, 1966) were less at Kaiteriteri. That the longevity of Kaiteriteri specimens was less than that of those of Kaikoura may also be a reflection of less favourable conditions at Kaiteriteri. Laboratory studies with fed and partially starved Evechinus (Section 10.3) showed that mortality of fed specimens was less. None of the fed but three of the partially starved urchins died during the experiments. Possibly, since fewer urchins were found in the shallow subtidal and intertidal areas than in deeper water at Kaikoura (Section 2.3), the deeper areas may be more suitable for Evechinus at this locality. This may also be reflected in the suggested differences in longevity of Kaikoura populations.

11.5 Summary

1. Various techniques for demonstrating growth rings in the hard parts of Evechinus were investigated. A method for showing growth rings in the test plates is described.

2. Growth lines were not found in the elements of Aristotle's lantern. Cycles of trabecular bands were found in sectioned spines but their possible correlation with age was not investigated.

3. Although growth bands may be demonstrated in any test plates only those of the apical system may be used for age determination; since the number of coronal plates increases with urchin size these plates are of unknown age.

4. Evidence which suggests that the aging technique is valid is presented.

5. After settlement and metamorphosis a light nucleus is laid down in the apical plates during the winter and early

spring. Each summer a dark band is formed, these alternating with light winter bands.

6. Annual growth of Kaikoura Evechinus was considerably greater than at Kaiteriteri. This may relate to differences in the food supply at each locality.

7. Laboratory growth was less than that observed in nature.

8. The strength of year classes varied considerably among Evechinus populations. Certain age groups were not represented in some populations and there was no overall trend of decreasing numbers with increasing age.

9. The longevity of Kaikoura Evechinus was typically greater than that at Kaiteriteri, and that of deeper populations at Kaikoura seemed greater than that of shallow subtidal and intertidal populations.

12. POPULATION SIZE STRUCTURES

12.1 Introduction

Differences between the size compositions of Evechinus populations studied were marked. Populations samples and observed during the present study showed the following patterns of size frequency distributions:

1. A spread of size, from juveniles to adults

(a) with large mean size (e.g. Wakatu Point, Fig. 43a and St Kilda Rocks, Fig. 41);

(b) with small mean size (e.g. Kaiteriteri, Fig. 43b and parts of Queen Charlotte Sound).

2. A restricted size range

(a) with large adults only (e.g. Seal Reef, Fig. 43c, Sharks Tooth Point and Third Bay, Fig. 44);

(b) with juveniles only (small numbers observed but not measured in a small area at Kaiteriteri and at Oaro, south of Kaikoura);

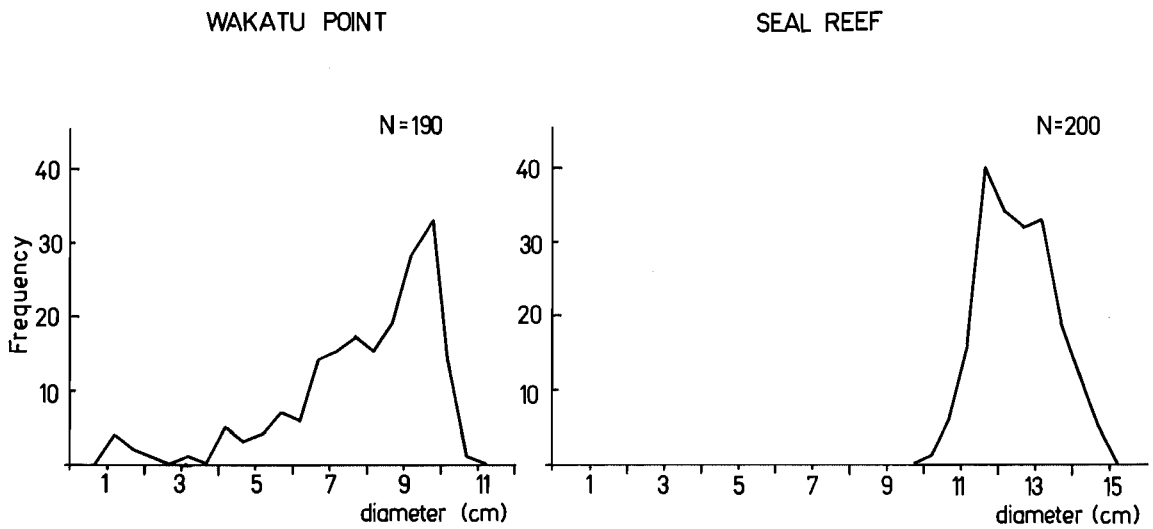
(c) with adults and juveniles but not medium sizes (e.g. Waeroa Point, Fig. 43d).

Most echinologists have investigated size frequency distributions to determine growth rates (Section 11.1) and some have noticed infra-specific variation in sizes (Buchanan, 1967; Ebert, 1968; Kawamura and Taki, 1965; Larsson, 1968; McPherson, 1965; Moore, 1935, 1937; Moore et al., 1963a). The causes of these differences, however, have not been extensively studied.

The present section considers how size structure variation may arise in Evechinus populations and attempts to relate this to the observations made. The main factors to be considered are:

1. Sampling. Do the measured samples represent the actual populations? This question is discussed later.

2. Generation of size structures. There appear to be six fundamental "generators", namely recruitment (in a broad sense), length of the breeding season, growth rate, longevity, rate of increase of the population and, in some cases, exploitation. Since


WAKATU POINT
N=190
Frequency
40
30
20
10
1
3
5
7
9
11
diameter (cm)
SEAL REEF
N=200
40
30
20
10
1
3
5
7
9
11
13
15
diameter (cm)

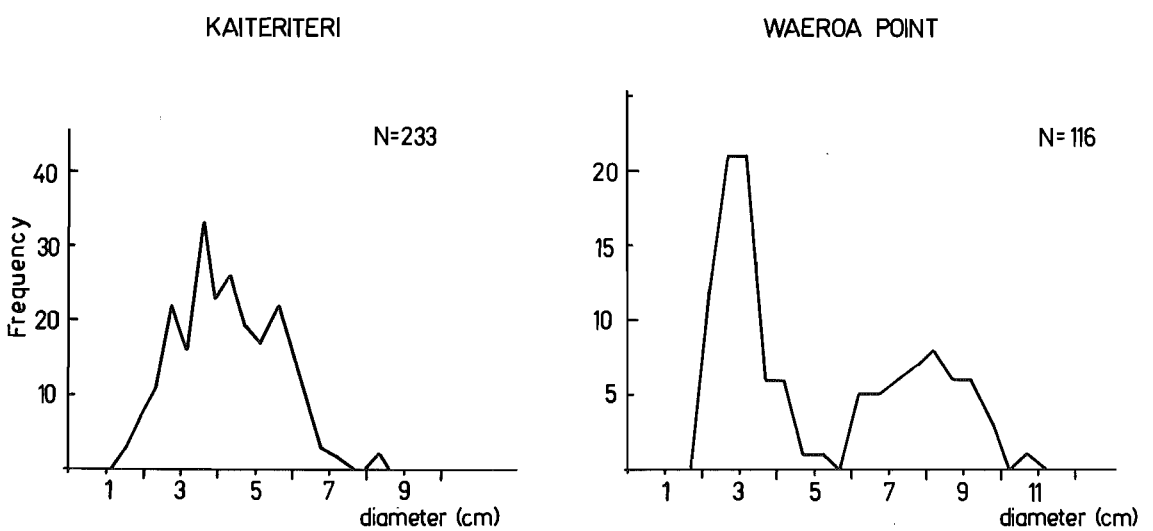
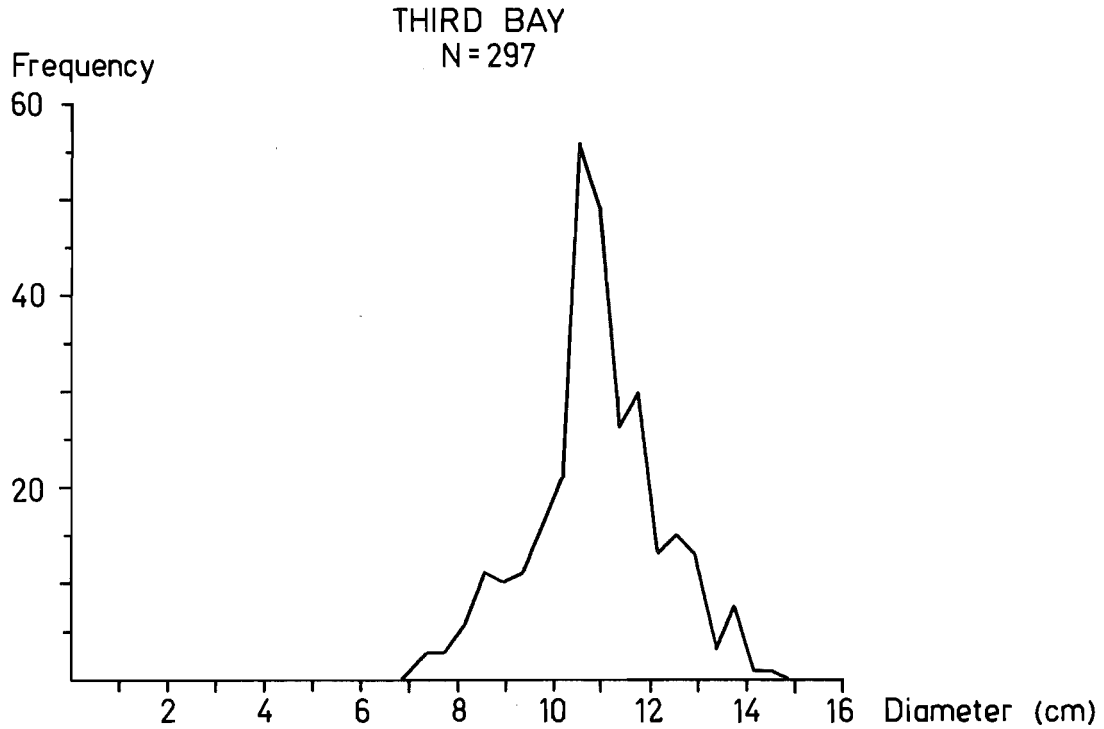

KAITERITERI
N=233
Frequency
40
30
20
10
1
3
5
7
9
diameter (cm)
WAEROA POINT
N=116
20
15
10
5
1
3
5
7
9
11
diameter (cm)

Figure 43

Diameter frequency distributions of Evechinus at (a) Wakatu Point, July 1967; (b) Kaiteriteri, November 1967; (c) Seal Reef, May and June 1967, and (d) Waeroa Point, March 1968.


THIRD BAY
N = 297
Frequency
60
40
20
2
4
6
8
10
12
14
16
Diameter (cm)

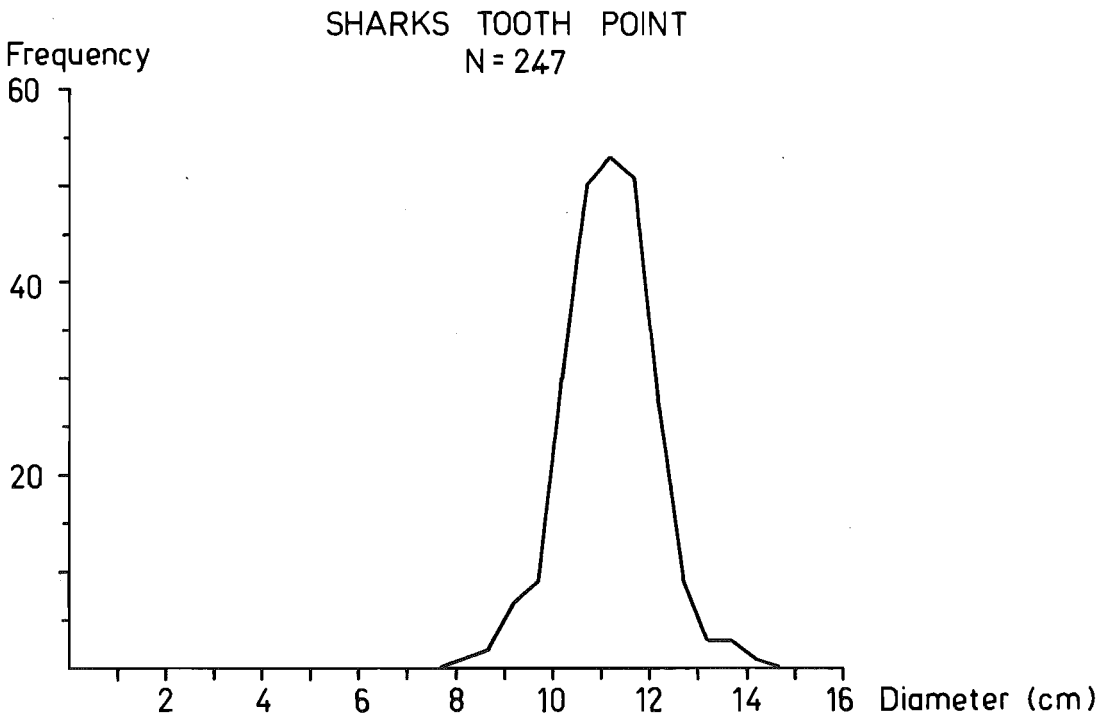

SHARKS TOOTH POINT
N = 247
Frequency
60
40
20
2
4
6
8
10
12
14
16
Diameter (cm)

Figure 44

Diameter frequency distributions of Evechinus at Third Bay, January 1968 and Sharks Tooth Point, January 1969.

most of these interact, simplified situations will be assumed to explain initially their effects on size distributions.

(a) Recruitment. Recruitment into a sampled population depends on the production of eggs (birth rate), larval survival and settlement, the survival of post-metamorphic animals, and their movements or migrations. The strength of size classes is partially dependent on the intensity of recruitment.

(b) Length of the breeding season. Larval recruitment from a population with restricted breeding is likely to occur over a shorter time than that from a population with extended breeding. Populations with restricted recruitment periods are likely to have more distinctly separated modes in size frequency distributions than populations with extended recruitment periods.

(c) Growth rate. Assuming that other factors are equal, more large animals are likely to be found in populations with higher growth rates than in those with lower growth rates.

(d) Longevity. If other factors are equal, larger animals are also likely to be found in populations with greater longevity than in those with lesser longevity.

(e) Rate of increase. An expanding population (positive rate of increase) is likely to have more smaller animals than a stationary or declining population.

(f) Exploitation. In a population subjected to exploitation, larger animals are likely to be selectively exploited so that if other factors are equal, a population subjected to greater exploitation will contain smaller animals than one subjected to less.

3. Resultant factors. Two may be considered, namely age structure and temporal changes in, or stability of size structures.

(a) Recruitment intensity and survival of recruits are reflected in the age structure of a population. For example, a poor year's settlement and/or survival will result in a poorly represented year class. Conversely, the existence of a poor year class suggests low success of settling and/or survival.

(b) Changes from year to year in the size structures of a

population suggest that one or more of the generators have changed.

All the above factors may now be further discussed, mainly in the light of information presented in previous parts of the thesis.

12.2 Discussion

1. Sampling.

As found by Larsson (1968) for Echinus esculentus, very small Evechinus are likely to be under-represented in all samples since they are typically very inconspicuous. This is probably true in spite of the fact that an endeavour was made to gain representative samples by using transects (Kaiteriteri, Novembers 1967 and 1968), transect and quadrats (Wakatu Point, July 1967), and quadrats (St Kilda Rocks, July 1968); and also by intensive searching in particular areas (Seal Reef, 1967-'68; Third Bay, 1968; Waeroa Point, March 1968; Sharks Tooth Point, January 1969, and Kaiteriteri, September 1967). This sampling bias is, however, unlikely to be significant in animals larger than about 3.0cm diameter.

Although very small individuals were probably under-represented, one can still discuss the size structure of the sampled part of a population. This corresponds with the "exploited phase" of fish populations considered, for example, by Beverton and Holt (1957).

2(a) Recruitment

i. Egg production

Although estimates were made of annual spawn volume for one breeding season (Section 10.3a), the relationship between egg production (birth rate) and larval recruitment was considered too complex for investigation in the present study. Possibly, since gonad volumes vary from year to year (Section 10.3a) egg production also varies. This alone is likely to result in irregular recruitment.

ii. Larval recruitment

Larval recruitment could not be studied directly as has been

done, for example, with polychaetes (Wisely, 1960), molluscs (De Blok and Geelen, 1958), and barnacles (Connell, 1961). But there is reason to suggest strongly that larval recruitment into any Evechinus population is probably irregular. Benthic invertebrates with short pelagic larval lives often show irregular larval recruitment, but the larval life span of Evechinus is farily prolonged, lasting about one month (Section 9.2). This increases the exposure of larvae to variable hazards, both biological and physical (Thorson, 1964, 1966). It seems highly unlikely, for example, that identical currents would carry the same number of larvae from a spawning population to a sampled population regularly each year. Even if they did, it is unlikely that other factors (e.g. predation) would operate identically.

Irregular larval recruitment may be a feature of many echinoderms. It has been suggested as a possibility for the echinoids Strongylocentrotus droebachiensis (Swan, 1961), S. purpuratus (Ebert, 1968), Lytechinus variegatus (Moore et al., 1963a), Paracentrotus lividus (Ebling et al., 1966; Kitching and Ebling, 1967), the sea star Luidia sarsi (Fenchel, 1965), and the holothuroid Cucumaria elongata, the ophiuroid Amphiura chiajei and the spatangoid Echinocardium cordatum (Buchanan, 1967).

iii. Survival

As no observations were made on settlement, the survival rate of early post-metamorphic animals could not be estimated. Thorson (1966) suggested that newly metamorphosed and settled benthic invertebrates "must pass a ... series of barriers". These barriers, which influence early survival, are probably not constant from year to year and thus recruitment from surviving post-metamorphic animals is also unlikely to be regular.

iv. Migration or movement

No evidence exists to suggest that extensive migrations of Evechinus occur. Adult movements, at least in larger animals, were very slight at Kaikoura (Section 9.3d) but probably more extensive

at Kaiteriteri. There is, however, no evidence to suggest migration of small animals into sampled populations. If such migrations occurred, one would expect to find populations containing predominantly small animals around populations containing predominantly large animals; the former were not located. Further, at Kaiteriteri, where detailed sampling was carried out in intertidal and nearby shallow subtidal regions, no marked differences between population size structures were observed (Figs. 35 and 40). In contrast, Larsson (1968) found that size tended to increase with depth in Echinus esculentus. He suggested that migration downwards might explain the observations. But an alternative explanation is in differences in the growth rates and survival of populations at different depths.

No influxes of small or medium sized Evechinus were observed into populations which were examined each month over a year (Seal Reef, May 1967 to April 1968; Kaiteriteri, November 1967 to November 1968).

(b) Breeding season

The breeding season of Evechinus is not extended, at least in the areas studied. Even though some spawning appeared to occur throughout the summer, peak spawning was restricted to late summer or early autumn at Kaikoura, and mid and late summer at Kaiteriteri (Section 10.3a). Taken alone, this might indicate that most larval recruitment probably occurs over a short time, although it is possible that more than one larval population could settle in a given area in one settlement season.

(c) Growth rate

Evechinus growth rates vary, the rates at Kaikoura being considerably greater than those at Kaiteriteri. Similar observations have been made for other echinoid species (Section 11.3).

(d) Longevity

Longevities may also typically vary among Evechinus populations. Kaikoura populations showed greater longevities than Kaiteriteri

populations (Section 11.4).

(e) Little is known of the rate of increase of the Evechinus populations studied. Possibly, since some populations showed predominantly old individuals (e.g. Seal Reef) while others showed large numbers of small individuals (e.g. Waeroa Point), some of the populations were declining while others were increasing.

(f) Exploitation

Although Evechinus populations are subjected to considerable human exploitation in some areas (e.g. intertidally, at Leigh, Auckland; W. J. Ballantine, pers. comm.) those of the study areas were not. Thus, in contrast to Tripneustes esculentus at Barbados (Lewis, 1958), exploitation has little bearing on interpretation of the size structures in the present study.

Resultant factors

(a) Age structure

Considering the species over a large area one would expect an overall trend of decreasing numbers with increasing age. However, in all sampled populations, year classes were represented to different degrees with some classes being absent. In no population was there an overall trend for decreasing numbers with increasing age; this trend would be expected in a self-supporting population with fairly regular recruitment. Further, the age structure of the Kaiteriteri population sampled in November 1968 differed from that of November 1967; 1+ years specimens, common in 1968, were not represented in 1967 (Section 11.4). These observations reinforce the above suggestions that larval recruitment intensity and survival vary from year to year.

(b) Temporal changes in size structures

Unfortunately, the study was not sufficiently prolonged to investigate the stability of, or changes in, population size structures over a period of several years as has been done for several echinoderms by Buchanan (1967). But the size structure of the

Kaiteriteri population sampled in Novembers 1967 and 1968 changed between years (Fig. 35). This suggests variation in recruitment intensity, independently suggested above, from age analysis of the small urchins in the population.

12.3 General discussion and conclusions

The above suggests that irregular larval recruitment and/or survival, absence of migrations, a fairly restricted breeding season, variations in growth rate, age structure and longevity, are all typical of the populations studied. This leads to variations in population size distributions (Figs. 35, 41, 43 and 44).

Of the observed size distributions, one might seek explanations for: (a) the absence of small and medium sized Evechinus in the Seal Reef pattern; (b) the absence of medium sized urchins at Waeroa Point; (c) the existence of larger animals at Kaikoura than at Kaiteriteri and (d) the absence of a series of distinct modes over the small diameters in the size distributions.

The absence of at least medium sized Evechinus at Seal Reef was probably real and unlikely to be a result of sampling bias. Animals examined appeared to be predominantly about 10 years old, suggesting that the population probably represented a single intensive settlement, possibly supported by smaller numbers from other settlements. Buchanan (1966) found also that a large population of the heart urchin Echinocardium cordatum was the result of a single intensive settlement.

The absence of medium sized animals at Waeroa Point was probably a result of a poor larval recruitment and/or survival four years prior to sampling (Fig. 42). The gaps in the November Kaiteriteri samples (Fig. 35) may be accounted for similarly. Presumably populations which showed a spread of size were the result of a series of successful larval recruitments.

The presence of larger urchins at Kaikoura than at Kaiteriteri seems mainly related to faster growth and greater longevity in the former area.

The absence of a distinct series of modes among smaller animals

in the populations is perhaps surprising since fairly restricted breeding seasons were suggested. A possible explanation is that smaller animals were typically under-represented in the samples; larger numbers of smaller animals might have indicated modes.

The foregoing has indicated a series of factors which appear to have a dominant influence on the size compositions of local Evechinus populations, and probably also populations of other marine benthic invertebrates. However, the direct study of some of the factors is difficult and the integration of all factors is necessarily complex.

12.4 Summary

1. Size frequency distributions show marked variations among Evechinus populations. Restricted size ranges are characteristic of many populations while a spread of size is present in others. Kaikoura urchins are typically larger than those at Kaiteriteri.

2. A series of factors, necessary for interpretation of size distributions, is examined. It is concluded that the dominant factor is probably settlement intensity although differences in growth rate and longevity are also important; Kaikoura urchins typically live longer and grow faster than those at Kaiteriteri, resulting in larger urchins at Kaikoura.

13. GENERAL DISCUSSION AND CONCLUSIONS

As with the general biology (Section 8) the population studies indicated considerable variation between the dynamics of urchins living in different areas. Differences between the major populations studied concerned

(a) extent of adult movements;
(b) reproduction;
  (i) patterns of seasonal changes in gonad index;
  (ii) spawn output;
  (iii) gametogenic cycles;
  (iv) spawning season;
  (v) size at sexual maturity, and
  (vi) sex ratio;
(c) age structure;
(d) growth rate;
(e) size structure.

Generalising, Kaikoura urchins may be regarded as fairly sedentary, fast growing and long lived, with highly productive gonads which reach a large size. In contrast, Kaiteriteri urchins are fairly mobile, slow growing and short lived, with low gonad productions and small gonad size.

The taxonomic characters outlined by McRae (1959) show that Kaikoura and Kaiteriteri urchins are, in fact, a single species. Although some genetic isolation may exist between the populations (despite probable widespread larval dispersal), most of the differences outlined above and in Section 8 appear to relate to environmental differences between the study areas.

Specifically, the lower gonad productivity, growth rate and longevity of Kaiteriteri urchins seem to relate mainly to the low algal species diversity and abundance in the area. At Kaikoura, with high algal species diversity and abundance, high gonad productivity, growth rate and longevity are found.

As found for the heart urchin Echinocardium cordatum (Buchanan, 1967) "numbers alone cannot be regarded as a good criterion for

ecologically optimum conditions." Evechinus appears to be adaptable and is able to live in abundance in environments which are not optimal for growth and survival. Possibly populations in such areas are recruited from the larvae of more productive populations.

Finally, the importance of studying the urchin in a variety of environments is emphasised from the markedly different biological features of populations living in different habitats.

ACKNOWLEDGEMENTS

Thanks are extended to my supervisors, Professor G. A. Knox and Dr. H. B. Wisely, for fostering independent thought and providing valuable criticisms.

For technical assistance I thank Mr L. D. Bowring who attended most of my dives and gave other field assistance; Mr B. M. Dukes for photography; Mr J. T. Kay for stores, and Mr A. Gall for workshop assistance.

Several divers, particularly Messrs J. Martin, G. C. B. Poore and D. W. Tattle, gave assistance, especially in survey work. Mr D. Ingram also recorded much information during diving in the Hauraki Gulf.

Mr P. Kettle kindly lent me his Nikonos underwater camera.

Sincere thanks are given to my parents for their encouragement and for the loan of an outboard motor which was essential for the study.

Thanks are given also to Miss Ann Hasney for typing the thesis.

The thesis was carried out while the author held a University Grants Committee Postgraduate Scholarship.

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APPENDIX 1. Morphometrics

The body component sizes of urchins are often expressed relative to total size to give a body component index (e.g. gonad index) where:

$$\text{Body component index} = \frac{k.\ \text{body component size}}{\text{total size}},$$

k being a constant. Since over certain size ranges some of the body component sizes increase in proportion to total size, the components of animals of different sizes may be compared by use of their indices.

Weight and volume are generally used to measure size. Choice between these for measurement of body components depends mainly on the type of organ being measured. Gonad volume is easier to measure than gonad weight but the gut is easier to measure as a weight. Volume is probably the best measure of total size, particularly if seasonal changes in component indices are being investigated; changes in the body components may be independent of total volume but not total weight.

Total volume (= test volume, usually of an intact urchin) may be measured by displacement but for large routine samples this method is laborious. Instead, regressions relating test volume to linear test measurements are generally constructed. Two linear test measurements were used in Evechinus; test height (h) and test diameter (d).

The volume of an ellipsoid with major axis, d and minor axis, h is

$K.\ d^2h$ where K is a constant.

The volume of a sphere with diameter, d is

$K'\ d^3$, where K' is a constant.

Since an urchin test is more similar to an ellipsoid than a sphere and since test height may vary with constant test diameter it was considered that regressions relating test volume to d^2h would give better estimates of volume than those relating test volume to d^3.

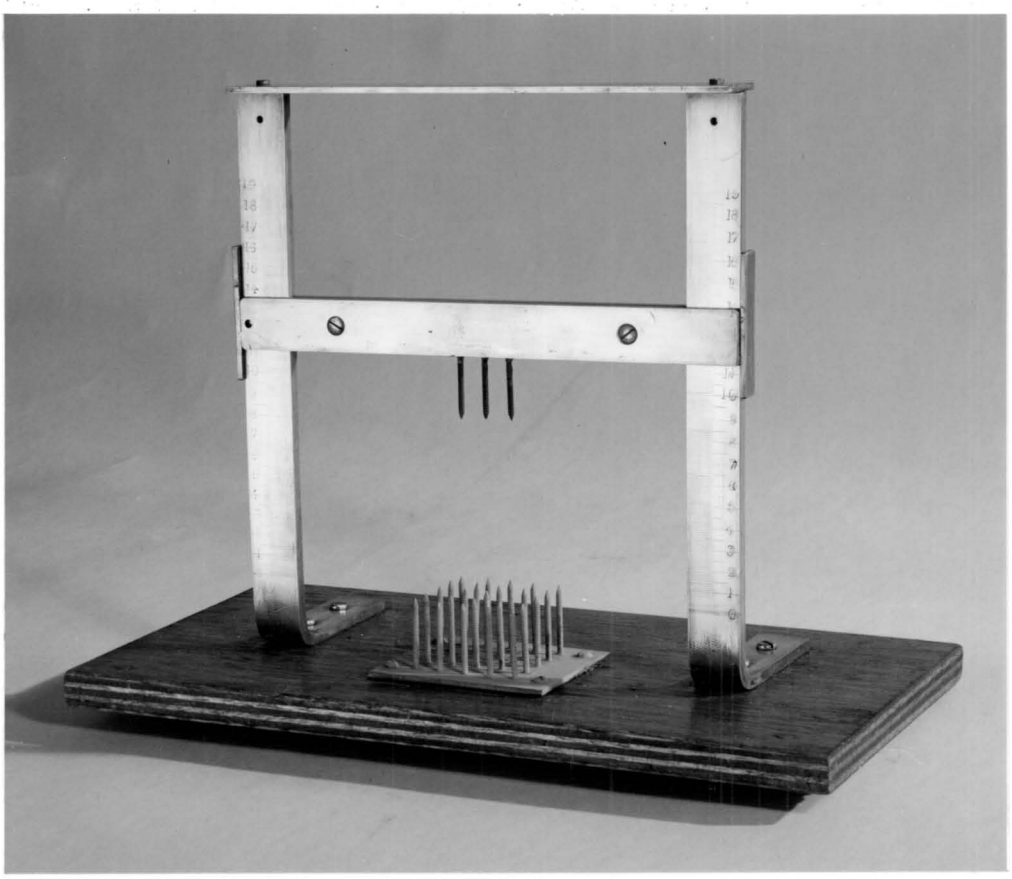
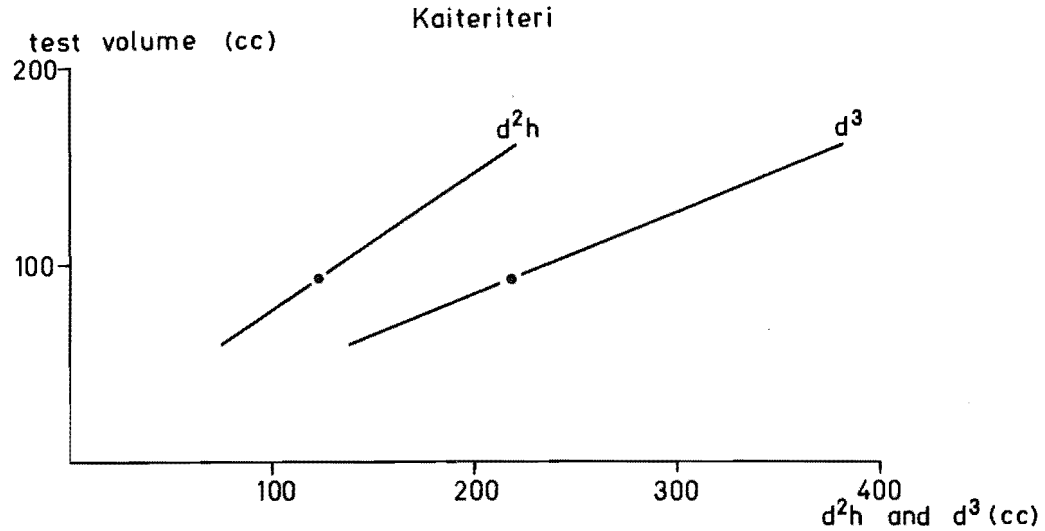


Plate 9

Apparatus used to measure height and diameter of Evechinus.
Photo, B. M. Dukes.

Calipers are generally used to measure test diameter and sometimes test height. However, in order to reduce time it was considered desirable in the present study to construct an instrument from which direct readings of both height and diameter could be obtained. The instrument designed is shown in Plate 9. The calibrated arms, top brace and sliding beam were of brass, the spikes were of phosphor bronze and the base was 7 thickness marine plywood. An urchin could be firmly placed on the bed of spikes and the beam could be lowered to measure test height. The urchin could then be placed vertically on a central base spike and the beam could be lowered to measure test diameter. Measurements could readily be made to the nearest millimeter although the instrument was more suitable for large than for small urchins. The instrument could have been improved by eliminating the two calibrated arms and having the top spike on a central calibrated slide which could have been fixed to the base by a large G- brace. Equalising measurements on each calibrated arm would not then have been necessary.

Least square regressions of test volume (V) on d^2h and d^3 were calculated for samples of 24 from Kaiteriteri and 75 from Wakatu Point, Kaikoura. Test volumes were measured in overflow vessels while heights and diameters were measured using the sliding beam instrument. The regressions are shown (Fig. 45), together with tests of significance of the regression coefficients, in Table 32. All regressions were highly significant, but as predicted above, volume was better estimated from d^2h than from d^3, as evident from the t values. Regressions of volume on d^2h were used in calculation of body component indices for Evechinus.


Kaiteriteri
test volume (cc)
200
100
d^2h
d^3
100
200
300
400
d^2h and d^3 (cc)

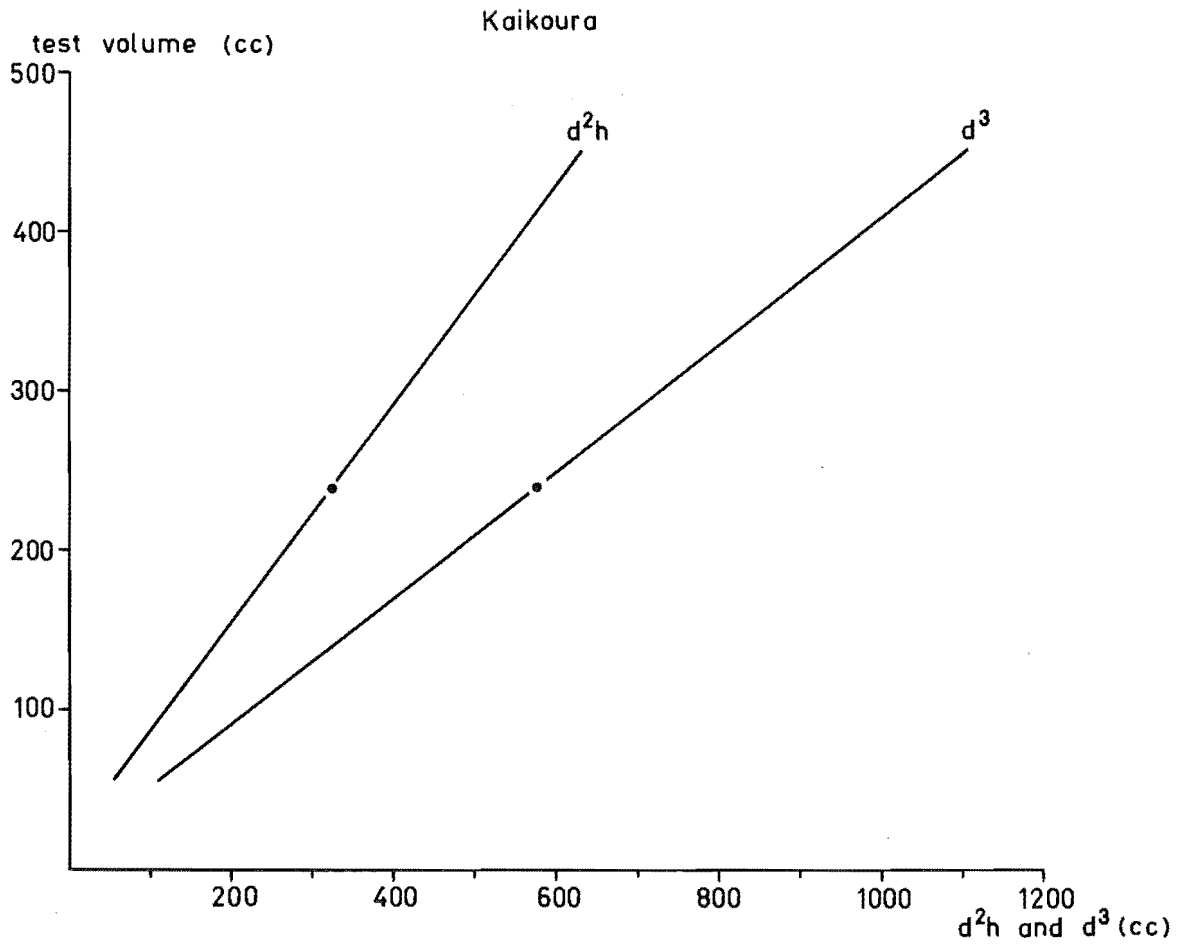

Kaikoura
test volume (cc)
500
400
300
200
100
d^2h
d^3
200
400
600
800
1000
1200
d^2h and d^3 (cc)

Figure 45

Least square regressions of test volume on d^2h and d^3 for samples from Kaiteriteri and Kaikoura. Lines extend over the ranges of sizes measured and means are indicated.

TABLE 32 : Least square regressions of test volume (V) on d^2h and on d^3 for samples from Kaiteriteri and Wakatu Point.

Locality	N	Regression equation	Test of significance t	P
Kaiteriteri	24	$V = 0.676d^2h + 8.625$	35.579	<0.001
		$V = 0.403d^3 + 3.892$	31.000	<0.001
Kaikoura	75	$V = 0.694d^2h + 15.396$	77.111	<0.001
		$V = 0.401d^3 + 8.993$	57.200	<0.001

APPENDIX 2. Commercial possibilities

Evechinus is at present exploited for food and, to a lesser extent, ornaments. Although it is sometimes sold within New Zealand for both these purposes, no major commercial exploitation is at present practised. This is evident from the approximate quantities (with corresponding values) taken by commercial fishermen during the years 1964 to 1968 (Table 33).

TABLE 33 : Approximate commercial quantities and value to the fishermen of Evechinus chloroticus, 1964 to 1967*

Year	Quantity		Value
	cwt.	Kilogram	$NZ
1964	176	8,941	692
1965	72	3,657	380
1966	104	5,283	870
1967	542	27,534	2237
1968	127	6,452	516

*figures supplied by the Marine Department, Head Office, Wellington.

The present section examines the commercial possibilities of Evechinus in terms of utilisation, fishing methods and possible regulations.

Utilisation

(a) Food. The gonads of sea urchins are commonly eaten in some countries and fairly intensive fishing is practised in Japan (Fuji, 1963, 1967), Barbados (Lewis, 1958), Chile (G. A. Knox, pers. comm.), and some Mediterranean and tropical countries (Harvey, 1956). Some urchin species are preferred over others, so basic to any question of similar exploitation of Evechinus is will they

be eaten?

Some New Zealanders, particularly Maoris, are extremely fond of Evechinus gonad. The author has had many people taste raw gonad for their first time and has found that opinions were extreme, from intense liking to equally intense revulsion. I have found, however, that many New Zealanders have not only never tasted urchin gonad, but they also have not been aware that it can be eaten. Making people aware of this food, particularly as a sea delicacy, may hold some possibilities.

Recently, Mr C. Mitcalfe advertised in a Christchurch newspaper to sell sea eggs (Evechinus). "He did not expect much response but was surprised at the results." (The Press, 22 February 1969; p.5). He sells these for $NZ4 a bag, slightly larger than a sugar bag. This might also indicate that there is a potential New Zealand market for the species.

Alternatively, Evechinus might be exported. Fuji (1967) has indicated that the annual yield of sea urchins in Japan has amounted to nearly 20,000 tons and that over-fishing has resulted in some areas. Possibly Evechinus gonad could be exported to this country.

Gonads are easily removed from the urchin and processing and preservation probably present few problems (Aust. Fish. Newsletter, December 1968).

The urchin is very abundant and the present study has indicated that areas producing high gonad productivity are likely to be densely weeded with a variety of macroscopic algae (e.g. Kaikoura Coast).

(b) Ornaments. Evechinus tests are on sale as ornaments in some New Zealand shops. Tests are also sold in other countries (Harvey, 1956). Most people agree that they are a beautiful ornament so that exploitation for this purpose might be profitable.

Spines are easily removed from the test (by brief boiling in water) and the denuded test is readily bleached in a solution of sodium hypochlorite.

Larger tests are generally preferred and this study indicates that they are most likely to be found in areas similar to those producing high gonad productivity.

Fishing methods

Diving, particularly using breathing apparatus is essential to efficiently exploit Evechinus populations. Although considerable numbers may be taken without breathing apparatus, the largest concentrations are often too deep to reach efficiently by snorkel diving.

The author has found that the most efficient method of gathering large numbers of urchins is to locate aggregations, mark these and/or lower a large wire basket ($1m^2$ x 30cm deep) to the sea bottom from a dinghy. The basket may then be filled and hauled into a dinghy. 100 urchins may thus be collected in less than 10mins diving in dense populations.

Possible regulations

Without knowledge of fishing intensity, and certain features of the ecology of Evechinus, discussion of possible regulations must be general. However, points to be considered are fishing season, minimum size of urchin, limit quantities, fishing localities and licencing of operators.

Restriction to exploitation might be imposed by limiting the fishing season as has been done for Strongylocentrotus intermedius (Kawamura, 1965) and Tripneustes esculentus (Lewis, 1958). A late spring and early summer season would probably be most suitable for Evechinus. At this time gonad is probably best suited and most efficiently exploited for food; the gonads are near peak size and are not as pulpy as when fully ripe.

There is probably little point in imposing minimum size limits since small urchins have very little or no gonad; they would therefore not be exploited for food (c.f. paua, Haliotis iris, and crayfish, Jasus edwardsii). Small urchins are also unlikely to be extensively exploited as ornaments. If size limits to prevent

exploitation of immature animals were imposed, these sizes would logically have to differ in different areas since urchins mature at different sizes in different areas.

Whether catches should be limited by imposing catch limits is not known. But from diving experience in several areas it is probable that some of these could withstand high exploitation rates. Although recolonisation of a particular area is likely to be chancy, other nearby areas might receive good recruitments.

Some conservation could be practised by limiting fishing to particular areas as has been done for Strongylocentrotus intermedius in Japan (Kawamura, 1965). These areas might serve to restock exploited areas.

As with most fisheries, licencing of operators would be necessary. If necessary, this would be a further method of reducing the exploitation rate.

Summary

Evechinus holds some commercial possibilities, mainly for food and for ornaments. Underwater breathing apparatus and a motorised dinghy would be essential for efficient fishing. If it were considered necessary to restrict exploitation this would probably best be done by firstly limiting the fishing season.